Feeding Rates, Parental Investment, and Brood Reduction in Caspian Terns (*Sterna caspia*)

James Scott Quinn
Department of Biological Sciences

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ABSTRACT

Fresh egg-weights and feeding rates to chicks were related to chick survival as one means of quantifying apportionment of parental investment within broods of Caspian Terns (Sterna caspia) at a colony in Georgian Bay, Lake Huron, during 1978 and 1979. First-laid eggs from 2-egg clutches were significantly heavier and usually hatched one to three days earlier than second-laid eggs in both years of the study.

In both years, first-hatched chicks were larger and generally better fed than second-hatched siblings. The disparity between feeding rates of first- and second-hatched chicks was greater in 1979. Brood feeding rates correlated positively with the percentage of food fed to the least-fed sibling through the period of B-chick ages zero to 10 days in 1978. I suggest that after this age period, parental control over which chick was fed diminished. In 1978, 10 of 16 second-hatched chicks were fed more than their older siblings during their first 5 days. This is interpreted as a parental response to reduce the competitive advantage of the larger first-hatched chicks.

Most chick losses were apparently caused by starvation or predation. In 1979, second-hatched chick disappearance (due to predation) was related to low feeding rates, whereas first-hatched chick disappearance was related to low fresh egg-weights. First-hatched chicks survived better than second-hatched chicks both years, and more pairs fledged two chicks in 1978. Maximum estimated feeding rates at the nest and fledging ages suggested that food was more available in 1978 than in 1979.

In 1979, second eggs apparently functioned as "insurance" eggs. When the first-laid egg failed to hatch, or the first-hatched chick died, the second-hatched chick was often successfully fledged. When first-hatched chicks survived, the second-hatched chick usually starved or was preyed upon, reducing the brood to one chick.

Parental investment patterns favored first-hatched chicks. Brood reduction, when employed, discouraged total nest failure, however, under appropriate conditions, brood reduction was avoided and full broods (or two chicks) were fledged.

To Kathie, my companion in 1978, center of my thoughts in 1979, with special thanks to an anonymous Pintail hen for assistance in transit to Jennifer's first full moon.

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INTRODUCTION

The importance of a clear theoretical framework fortthe study of mate choice, parental care, and reproductive success has been apparent for over a century (Darwin 1871, Fisher 1958, Hamilton 1963, 1964, Williams 1966, Trivers 1972, 1974, Alexander 1974, Wilson 1975, Emlen and Oring 1977). Theoretical treatment of parental care has improved since Triver's (1972, pp. 139) working definition of parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of a parent's ability to invest in other offspring." My thesis investigates apportionment of parental investment within broods of Caspian Terns as it relates to brood reduction.

A. Evolution of Clutch Size

The numbers of offspring among which parental investment must be apportioned is determined by the size and number of clutches or litters. Clutch size and parental investment within clutches is of considerable importance to the reproductive success of birds. Sective pressures such as predation and food limitation come to bear on clutch size determination.

Various authors (e.g., Cody 1966, Perrins 1977) have pointed out the potential importance of predator pressure in limiting clutch size, especially in species that rely on crypsis for predator avoidance. Feeding visitation rate increases by parents, and begging calls from additional chicks in larger broods may attract predators. Predation pressure may limit clutch size in certain species, however, this effect may be unimportant for many species.

Lack (1954) reviewed hypotheses concerning clutch size determination and concluded that the modal clutch size results from natural selection for the largest brood size that parents can feed well until independence. He cited data from two species of swifts showing that larger than average clutch sizes did not result in increased fledging success.

Parental survival to the next breeding attempt is also important to lifetime reproductive success of iteroparous species. Cody (1971) reviewed some examples of breeding costs in terms of parental survival. Goodman (1974) used seabird life table parameters to calculate that where reproductive effort exposes a parent to risks, it must be compensated for by increased fledging success at least 19 times the fractional reduction of parental survival probability.

Charnov and Krebs (1974) developed a model accounting for parental and juvenile survival probabilities as well as the seasonal reproductive success by parents according to clutch size. The optimal clutch size predicted was less than the most productive because of deleterious effects on parental (and juvenile) survival associated with larger clutches. A possible extension of Charnov and Krebs' hypothesis predicts that parents might adjust their reproductive effort according to their own age-dependent life expectancies (Gadgil and Bossert 1970, Pianka and Parker 1975, Stearns 1976). Although mortality rates of adult birds appear not to be age-dependent (Cody 1971), these data are based on band returns which may have a bias associated with band losses (Kadlec and Drury 1968). In addition, age-dependent differences in parental abilities such as foraging (see Orians 1969, Recher and Recher 1969, Buckley and Buckley 1974, Verbeek 1977, Searcy 1978) may allow increased clutch sizes at a reduced cost to parental survival.

The importance of extended parental care and associated offspring quality, especially in species with specialized feeding habits and considerable intra-specific competition, was stressed by Amadon (1964) and Brockelman (1975). "Higher quality" offspring stand a greater chance of surviving to reproduce, hence are more valuable to parental fitness. Andersson (1977) hypothesized that as clutch (brood) size increases above a certain threshold, reproductive success may be reduced as a result of reduced offspring quality, increased age of first breeding, or reduced fledging success.

Thus, there are numerous trade-offs involved in clutch size evolution such as number of offspring produced, "quality" of offspring raised, and likelihood of parental survival to breed again. Experiments involving addition of eggs or chicks to produce larger than normal broods (brood packing experiments) provide evidence indicating the relative importance of these trade-offs. Lack (1966) cited brood packing experiments indicating that artifically increased broods did not have increased per pair fledging success in swifts (Apus spp.), Manx Shearwater (Puffinus puffinus), Laysan Albatross (Diomedea immutabilis), and Leache's Stormpetrel (Oceanodrama leucorhoa). Apparently in these species the number of offspring produced by an average size clutch is optimal. Askenmo (1977) found expanded broods of Pied Flycatchers (Ficedula hypoleuca) were no more productive numerically than normal broods and produced lighter chicks at fledging (likely resulting in decreased survivorship). Furthermore, weight loss (which may imply decreased survivorship) during the breeding season may be greater for female parents with enlarged broods (e.g., Askenmo 1977). On the other hand, a study of brood packing in Tree Swallows (Tachycineta bicolor) found no differences in maternal weight loss or fledgling

survivorship relative to control nests, and more young were fledged from enlarged broods relative to normal ones (De Steven 1980). Similarly, Gannets (Sula bassana), which normally lay one egg but are capable of re-laying, fledged more chicks per pair when clutches were artificially enlarged to two eggs (Nelson 1964). Red-winged Blackbirds (Agelaius phoeniceus) with packed broods produced more chicks than normal broods, although the chicks were lighter weight (Cronmiller and Thompson 1980).

Charnov and Krebs (1974) expected adult survival to be more important in long-lived species, and cited a study of Glaucous-winged Gulls (Larus glaucescens), indicating that the most productive clutch size was larger than the mode (Ward 1973, cited in Charnov and Krebs 1974). Haymes and Morris (1977) found that enlarged broods of Herring Gulls (Larus argentatus) fledged more chicks than normal broods, and had offspring of comparable weight and viability prior to fledging. However, these authors suggested that locally abundant, artificial food sources may have been responsible for weight and viability similarities.

B. Effects of Age and Experience on Breeding

Interpretation of clutch size comparisons is difficult because of the influence of parental age and experience. Parental "quality" affects several breeding parameters. Older and/or more experienced birds may breed earlier in the season (e.g., Black-legged Kittiwake, Rissa tridactylus, Coulson and White, 1958, Coulson 1966; Parasitic Jaeger, Stercorarius parasiticus, Davis 1976; Red-billed Gull, Larus Novaehollandiae, Mills 1973). Previous breeding experience with the present mate may further augment breeding success. Red-billed Gulls (Mills 1973) and Black-legged Kittiwakes (Coulson 1966) retaining their mates from the previous season initiated clutches earlier and showed higher mean fledging rates than

those changing mates between seasons.

Clutches initiated later in the season show declining clutch size in many species, including Ring-billed Gulls (larus delawarensis, Ryder 1975), Herring Gulls (Parsons 1975a), Red-billed Gulls (Mills 1979), Arctic Terns (Sterna paradisaea, Lemmetyinen 1973a), and Caspian Terns (Soikkeli 1973a).

Another component of parental investment, egg weight or volume, may decline with seasonally later breeding (e.g., Herring Gulls, Parsons 1972, Davis 1975; Black-legged Kittiwakes, Coulson and Thomas 1978). Declines in Herring Gull egg size occured despite probable improvements in food availability as the season progressed (Parsons 1975a).

Reproductive success may vary with breeding dates and parental age. Haymes and Morris (1977) reported better fledging success for early-nesting Herring Gull pairs. Immature plummaged Brown Pelicans (Pelecanus occidentalis) had reduced clutch sizes and breeding success relative to mature breeders (Blus and Keahey 1978).

The effects of seasonality and parental age and/or experience are difficult to separate. Herring Gull parental age does not fully account for seasonal differences in clutch size and egg size (Parsons 1976). Mills (1979) concluded that for Red-billed Gulls, foraging ability and food availability are the important factors controlling egg and clutch sizes, however, this explanation is not universal (see Parsons 1975a, Coulson and Thomas 1978).

C. Parental Investment Apportionment

Parental investment by definition is measured in terms of costs to other offspring, both present and future. In seasonally reproducing birds, effects of parental investment are probably much greater among members of the same brood compared with those between members of sequential broods. Apportionment of parental investment among a brood

(i.e., the distribution of parental resources such as materials for egg formation or food or other aspects of parental care) is also logistically easier to study. In species with non-precocial young, chick feeding is the most important component of parental investment allowing differential costs and benefits to brood members. Assuming that parents invest in offspring according to limits imposed by food availability, the nature of food resources should shape both parental investment and chick growth patterns. O'Connor (1977a, 1977b) described three brood-growth patterns in representative passerine species: 1. clutch size adjustment where food supplies are predictable (e.g., Blue Tit, Parus caeruleus; temperature at laying correlates with prey abundance at chick hatching); 2. brood reduction where food supplies for chick feeding are unpredictable at egg laying but stable over the nesting period (e.g., House Sparrow, Passer domesticus); 3. resource storage (as fat or other food reserves not channeled into growth) when food levels fluctuate during the nesting period (e.g., House Martin, Delichon urbica). Often a combination of these patterns best suits the environment (O'Connor 1977a).

Brood reduction can be facilitated by parents by initiating incubation of eggs prior to clutch completion, thus establishing a size hierarchy among brood members through asynchronous hatching (Lack 1954). Asynchronous hatching is well known in many avian species (Lack 1968, O'Connor 1978). Parent birds may distinguish their young using size differences, and distribute food accordingly, selectively starving the youngest when food supplies are short (Ricklefs 1965). Size differences allow for an increased competitive ability in chicks hatched early among a brood. Fighting among siblings, with an advantage to larger chicks in a brood, may establish a dominance order relating to food distribution in certain species (Newton 1977, Werschkul 1979). The above mentioned factors affect

the survival of individual brood members differentially. Reduced survival of chicks hatching late among a brood has been reported in many avian species (e.g., Hawksley 1957, Ricklefs 1965, Parsons 1970, 1975b, Langham 1972, Young 1978, Lundberg and Väisänen 1979, Raye and Burger 1979, Werschkul 1979).

Egg weights may decline with laying order (e.g., Herring Gulls, Parsons 1975a, 1976; Red-billed Gulls, Mills 1979; Laughing Gulls, Larus atricilla, Ricklefs et al. 1978; some eagles, Newton 1977), though first and second eggs may be statistically similar (e.g., Herring Gulls, Parsons 1975a; Red-billed Gulls, Mills 1979). The importance of Herring Gull egg size and hatching order to chick survival has been investigated (Parsons 1975a). Egg switching experiments were used, establishing clutches in which third eggs hatched first and first eggs hatched last (Parsons 1975a). Parsons (1975a) found that hatching order was important to chick survival, however, some differential mortality was attributed to egg size differences. Several studies found that independent of hatching order, increased egg size (dimensions and weight) is of survival value to chicks (e.g., Common Terns, Sterna hirundo, Nisbet 1973; Herring Gulls, Parsons 1970; Snow Geese, Anser caerulescens, Ankney 1980; European Swifts, Apus apus, O'Connor 1979). However, Davis (1975) suggested that the increased survival could be a function of parental age and experience rather than egg-size. To eliminate confounding effects of parental "quality," Nisbet (1978) performed egg exchanges among Common Tern and Roseate Tern (Sterna dougallii) clutches. In this manner he showed that increased egg size alone can contribute to chick survival.

Some authors have investigated differences in egg components related to egg size or weight. Egg weight correlated positively with the amount

of yolk in Laughing Gulls and Japanese Quail (Coturnix japonica), however, a logarithmic regression showed that the proportion of yolk declines significantly as egg size increased (Ricklefs et al. 1978). Variation in egg size within clutches was due mainly to differences in albumen content as opposed to yolk in Herring Gull (Parsons 1972) and Common Tern (Nisbet 1978) eggs.

Egg size differences as a function of laying order are probably not solely due to a depletion of egg production materials (Parsons 1976). In Herring Gulls, when first eggs were removed immediately after they were laid, third eggs were larger than third eggs from control nests (Parsons 1976). The advantage in laying a small last egg (Herring Gulls usually lay three eggs) may be the ease of brood reduction when it is necessary. The small last chick would be easily out-competed for food by its brood mates, thus reducing the cost of brood reduction. Large Laughing Gull eggs produced large bodied chicks with disproportionately high water levels (Ricklefs et al. 1978). Larger body size and high water reserves may facilitate increased competitive capabilities and better resistance to dehydration (Ricklefs et al. 1978).

Those chicks that hatch early among a brood may be relatively large when they hatch (because of egg size difference) and will have a head start at growth before the younger sibling or siblings hatch. Larger chicks are better at competing among brood members for food. Chick growth rates are often slowest for last hatched chicks (e.g., European Sparrow Hawks, Accipiter nisus, Moss 1979; Marsh Hawks, Circus cyaneus, Picozzi 1980; Common Terns, Langham 1972; Little Blue Herons, Werschkul 1979; Red-winged Blackbirds, Strehl 1978).

O'Connor (1978) reviewed the literature pertinent to brood reduction

in food limited bird species and presented a general theory of brood reduction based on inclusive fitness (Hamilton 1964). He predicted that brood reduction would be favored by the victim (chick to be eliminated), the survivor(s) (members of the brood remaining alive following reduction), and the parents according to different "thresholds," which are based on the chicks' probability of subsequent survival and reproductive success. Survivors and victims are related to themselves by one and to siblings by one-half and parents are related to all offspring by one-half (i.e., the probability of sharing a gene with oneself is one, with one's sibling is one-half, and with one's offspring is one-half). Therefore, during a food shortage of increasing severity, survivors should favor brood reduction first, then parents, and finally victims (O'Connor 1978). Furthermore, the differences between the brood reduction thresholds of survivors and parents should be greatest in small broods (O'Connor 1978), suggesting a possible case of parent-offspring conflict (Trivers 1974, Alexander 1974). Trivers (1974) promoted psychological manipulation by offspring, while Alexander (1974) stressed parental manipulation as important factors in parent-offspring conflict. According to Trivers (1974), offspring may attain extra parental investment by using psychological ploys, such as exaggerated begging for food. Computer models (Parker and McNair 1979, McNair and Parker 1979) showed that genes for exaggerated begging by chicks could spread in a population. They showed, however, that the most likely co-evolutionary outcome (considering parental "retaliation") would be a compromise between the optimum amount of food for the "greedy" chick(s) and the optimum distribution of food for the parents' reproductive success. This compromise was anticipated by Dawkins (1976).

D. Research Subject and Objectives

Caspian Terns (sub-family Sterninae), which share with gulls the family Laridae of the order Charadriiformes, are the largest of the terns. The species has a widespread yet disjunct distribution, nesting on all continents except South America and Antarctica.

The courtship of Caspian Terns has been described (Bergman 1953) and is similar to that of Common Terns (Palmer 1941). Most aspects of courtship are performed by both sexes and courtship feeding is an important component (Bergman 1953).

The nest is merely a scrape in the substrate that is sometimes lined with vegetation (Ludwig 1965). It is formed by scraping movements with the feet by both members of the pair (Bergman 1953). The area around the nest defended by pairs in Great Lakes colonies measured 1.1 to 1.5 m^2 (Ludwig 1965).

Clutch sizes are typically one to three eggs although the frequencies vary according to colony location. One and two-egg clutches are common in Lake Winnipeg (O'Donoghue and Gowanlock 1919, Evans et al. 1970) and California (DeGroot 1931, Miller 1943), while two and three-egg clutches are most frequent in northern Europe (Bergman 1953, Soikkeli 1973a) and the Great Lakes (Ludwig 1965, Shugart et al 1978). Incubation duties are shared (Bergman 1953) and the incubation period in the Great Lakes is about 26 days (Ludwig 1965). After hatching, chicks are brooded during the first few days and both parents feed the chicks (Bergman 1953). According to Koli and Soikkeli (1974), chicks were fed the same size and species of fish that adults themselves eat. Caspian Terns in Finland (Koli and Soikkeli 1974) and the Great Lakes (Allen 1977, Ludwig 1965) are reported to eat fish exclusively. Vermeer (1973) reported infrequent

occurrences of insects, egg shells, and bird bones in Lake Winnipeg Caspian Tern pellets (regurgitated balls of undigested material). Fish prey are carried to the nest individually in the bill and swallowed whole by the chicks (Bergman 1953).

Parental care extends beyond the age of fledging (first flight) and, at least in Poland, Caspian Terns migrate to the wintering grounds in family groups (Jozefik 1969). Great Lakes Caspian Terns winter mainly in the Gulf of Mexico and along the southeastern U.S. Atlantic seaboard as well as northern South America and Caribbean Islands (Ludwig 1942, Ludwig 1965). Immature Caspian Terns spend their first full year on the "wintering" areas (Ludwig 1965). Caspian Terns tend to return to the region of their natal colony to breed (Shugart et al. 1978).

The Great Lakes Caspian Tern population declined slowly from 1925 to 1959, then increased from 1960 to 1964, presumably in response to the invasion and subsequent increase in Alewife (Alosa pseudohaerengus) populations in the Great Lakes (Ludwig 1965). The increase in Caspian Tern numbers continued in the U.S. Great Lakes from 1965 to 1967 and between 1967 and 1976 an increase of 11 % of nesting adults were reported, however, the population stabilized between 1976 and 1978 (Shugart et al. 1978).

The Caspian Tern colony on the South Limestone Islands was first recorded in 1927, and banding activities and records suggest that the colony has been active continuously since then (Ludwig 1965). Population estimates for the South Limestone Islands Caspian Terns were 200 breeding pairs in 1961 and 150 pairs from 1962 to 1964 (Ludwig 1965). More recent estimates are not available in the literature.

The objective of my research was to study the reproductive ecology of Caspian Terns on the South Limestone Islands. I have limited the aims of

this thesis to the following: 1.) estimating apportionment of parental investment according to laying order, 2.) examining the relationship between feeding rates of chicks, and food availability and feeding apportionment within broods, and 3.) determining survivorship parameters as they vary with hatching order, particularly as that relates to brood reduction.

MATERIALS AND METHODS

The Study Islands

The study was done on the South Limestone Islands, during the spring and summer of 1978 and 1979. The island chain was approximately 65 ha, located about 50 km north-west of Parry Sound, Ontario, in Georgian Bay (45^{o} 23' N, 80^{o} 32' W). A backbone ridge of limestone gravel runs roughly north-west to south-east on the main island, and two limestone gravel knolls of about 300 m^2 are on the northernmost island.

Several non-avian terrestrial vertebrates were sighted in the course of the study including the Beaver (Castor canadensis), Meadow Vole (Microtus pennsylvanicus), Silver-haired bat (Lasionycteris noctivagens), Northern Water Snake (Natrix sipedon sipedon), Northern Brown Snake (Storeria dekayi dekayi), and Eastern Garter Snake (Thamnophis sirtalis sirtalis).

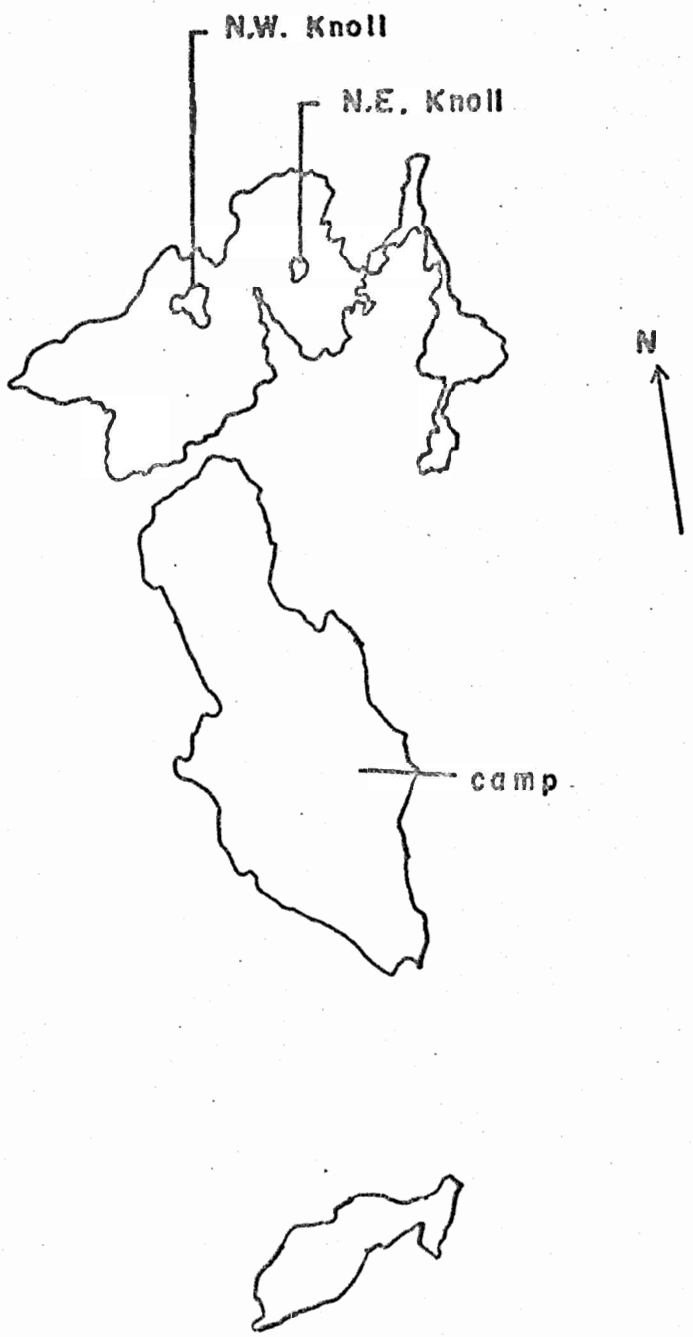
Avian species nesting on the island chain were the Yellow Warbler (Dendroica petechia), Song Sparrow (Zonotrichia melodia), Tree Swallow, Red-winged Blackbird, Red-breasted Merganser (Mergus serrator), Blue-winged Teal (Anas discors), Mallard (Anas platyrhynchos), Pintail (Anas acuta), Spotted Sandpiper (Tringa macularia), Herring Gull, Ring-billed Gull, and Caspian Tern. Ring-billed Gulls were most abundant, estimated at 4,500 pairs in 1960 (Ludwig 1962). Herring Gulls numbered about 193 nesting pairs in 1978 (pers. obs.).

Caspian Terns nested in two separate areas on the northernmost island (Fig 1). Intensively studied nests were located on a gravel knoll (North-east knoll) and were surrounded by Ring-billed Gull nests. Caspian Terns also nested on mats of Sedum acre (growing on the limestone bedrock) and along the west edge of a second knoll (the north-west knoll) on the same island (Fig 1). Ring-billed Gulls nested along the eastern edge of this

Figure 1

The map[1] of the South Limestone Islands chain

[1] Redrawn from an undated aerial photograph



1 cm = 82.9 m

Caspian Tern nesting area and Herring Gulls nested to the south and north-west.

A camp was established on the main island (Fig 1) and occupied from 4 May to 15 August 1978 and from 23 April to 15 August 1979.

The Study Site

The substrate of the north-east knoll was limestone gravel with a thin layer of fish bones (from regurgitated pellets) covering the tern nesting area. Vegetation on the knoll consisted of Agropyron trachycaulum var. glaucum, Chenopodium album, Potentilla norvegica, Malva neglecta, Achillea millefolium and Urtica dioica. Ring-billed Gulls nested surrounding the knoll in dense stands of Urtica dioica. Caspian Terns most frequently nested in the open areas on the top of the knoll. The same general area of the knoll was studied both years, however, the 1978 study area was larger ($\doteq$ 230 m^2) than the 1979 study area ($\doteq$ 160 m^2).

METHODS

Nest Checks

Nest checks in 1978 were made every other day from 4 May until 27 June, and every four days thereafter, weather permitting. In 1979, nest checks were made every other day from 4 May until 28 June, and every four days thereafter, weather permitting.

Numbered wooden stakes ($\doteq$ 1 M long) were positioned about 25 cm from the edge of the nest, after the first egg was laid. First-laid eggs were called A-eggs, second-laid B-eggs, and third-laid C-eggs, and were marked with non-toxic felt-tipped markers. Nest contents were recorded during nest checks, however in 1978, egg disappearance dates were not always recorded since empty nests were sometimes missed that year.

Pipping and hatching dates were recorded both years. It usually took one day for pipping eggs to hatch. Sixteen eggs from non-study nests (north-west knoll) were checked daily after pipping (small hole through the shell). Fifteen of those hatched one day after pipping and one hatched two days after pipping. Since study area nests were checked every other day, hatching dates were determined as the day following pipping, except when pipping occurred on the day between nest checks. In that case, hatch date was the first date a chick was found in the nest. In 1979, fresh eggs were weighed using a 100g pesola spring scale (Bleitz Wildlife Foundation, Hollywood). During the 1979 nest checks, study nests with eggs were covered by nest domes (a steel ring about 40 cm in diameter was the base for the ½" chicken wire dome) for protection against Ring-billed Gull egg predation. Nest domes were removed on investigator departure from the colony.

Chicks were designated according to the egg of origin. When both A and B-eggs hatched in the same interval between nest checks, hatching order was assigned according to dampness (if one chick was damp it was designated the B-chick) or size (when neither were damp, the largest chick was designated the A-chick). In 1978, chicks were differentially dyed, with Rhodamine-B in 95% ethanol, according to hatching order (A-chicks dyed on the crown, B-chicks on the throat, C-chicks on both wings). In 1979, A-chicks from even numbered nests were dyed on the crown, with Malachite green in isopropyl, while the B-siblings were dyed on the foot. The dye schedule was reversed for chicks from odd numbered nests.

In 1978, chicks were banded with USFWS bands by age 4 days. In 1979, chicks were banded before age 8 days with unique combinations of color bands and one USFWS band.

In 1979, exposed culmen lengths of all newly hatched chicks were measured. A-chicks were measured a second time after the B-siblings hatched. Beginning on 28 June 1979, all chicks' culmen lengths were measured during most nest checks.

On 1 June 1978, to restrict chick mobility during nest checks, a collapsible fence of polyethalene sheeting (0.5 m high) held up by wooden stakes was erected around the nesting terns, enclosing an area of about 230 m^2. The fence was set up before each nest check and taken down afterwards until 4 July when it was stapled up permanently. On 13 June, 1979, a chickenwire fence supported by wooden stakes was erected around the area of 162 m^2.

Chicks' fates were recorded during each nest check, and dead chicks removed for autopsy. Autopsies included an external examination for signs of injury, examination of the mouth lining and throat for parasites (Hirudinea), an internal examination of stomach contents, and, for young chicks, a determination of the presence or absence and size of a yoks sac.

Chicks present and alive until at least age 30 days were considered fledged. Some broods left the study area prior to the installation of the permanent fence on 4 July 1978. Chicks of ages 12-23 days which disappeared prior to 4 July were classified as fate "unknown." Chicks of ages 24-29 days which disappeared from the study area prior to 4 July were classified "probably fledged."

Feeding Rate Observations

Feeding rates to chicks were observed in both years from a 1.2m x 1.2m x 1.2m plywood blind elevated 1.2m off the ground, positioned about 17m from the nearest nests. Study area vegetation was trimmed as necessary during nest checks to facilitate viewing.

All-day watches were used to determine periods of peak chick-feeding activity. Based on these data, blind observation times were 07:30 - 10:00 and 18:30 - 21:00 hours in 1978 and 06:15 - 09:15, and 17:45 - 20:45 in 1979.

Observation techniques used during feeding watches in 1978 were as follows. One person (the observer) scanned the study area with seven x 35 mm or eight x 40 mm binoculars watching adults on the ground carrying fish and watching for adults flying in carrying fish. When a chick feeding occurred, the observer would describe the feeding to a second person (the recorder) who recorded it in a field book. Data reported included nest number, chick fed (A, B, C), species of fish, and length of fish in units of adult bill length (e.g., 1.5 times the adults' culmen length). A more efficient observation technique was used in 1979. Both workers (observers) used binoculars and clipboards with mimeographed data collection tables. Each observer scanned half of the study area watching adults on the ground carrying fish, and watching for adults flying in carrying fish. When a chick feeding occurred, the observer watching informed the other observer who would scan the whole area. If one observer was recording or finishing a feeding observation when the second observer announced a chick feeding in progress, the first observer began scanning the study area, and recorded the previous feeding data later. When feedings were too frequent to simultaneously observe and record, a cassette tape recorder was used to record descriptions of feedings verbally.

A spotting scope (20 x eyepiece) was used to identify unfamiliar fish when time permitted. Fish previously unfamiliar were collected when found during nest checks, and identified (Scott and Crossman, 1973). By the start of the chick feeding period, observers were familiar with

most prey species through observations of courtship feeding earlier in the season.

Since prey lengths were determined according to adult culmen lengths, it was necessary to establish a standard mean adult exposed culmen length (Appendix 1). The standard mean exposed culmen length used was 6.81 cm. This length was used to convert prey length from units of adult bill lengths to centimeters.

Fish-prey weights were estimated using weight-length relationships of the species of fish most commonly fed to chicks. Weight and length data for Alewifes (Alosa pseudoharengus), Rainbow Smelt (Osmerus mordax), Rock Bass (Ambloplites rupestris), Small-mouth Bass (Micropterus dolomieui) and Yellow Perch (Perca flavescens) from South Bay, Lake Huron, were obtained from the Ontario Ministry of Natural Resources, Tehkummah, Ontario. The data were fitted to exponential curves and plotted on a non-logarithmic scale, weight (g) versus length (cm) with all correlations higly significant (Appendix Table 1). All complete records of feedings involving the above mentioned species of fish were converted to weights using the weight-length curves. In 1978, 83.3% (n=414) of clearly observed chick feedings were of species for which length-weight curves had been generated, while in 1979 the corresponding value was 80.3% (n=175). Fish species for which weight-length curves were not available (both known and unknown species) were assigned weights by using weight-length relationships of similar shaped fish. When fish length and/or species (or body shape) were missed, prey weights were assigned using the following methods:

A) Length and species (or body shape) unknown. The mean prey weight fed to chicks of that age (the age when the unknown feeding occurred) was assigned.

B) Species (or body shape) known but length unknown. The mean weight of the species fed to chicks of that age (the age when the feeding occurred) was assigned.

C) Length known but species (or body shape) unknown. The weight assigned was based on the average weight of prey of the recorded length fed to chicks of that age (the age when the feeding occurred).

Time-lapse Filming

During both years, a super-8 mm movie camera equipped with a seven to 70 mm lens was mounted on a tripod, in a blind similar to that used for observations and erected adjacent to it (in 1978). A solenoid fixed to the camera and powered by a 12-volt battery was pre-set for single-frame operation at the rate of about one frame per 10 seconds. In 1979, a photocell was installed so that the camera began filming when sufficient light became available at dawn, and stopped when light became insufficient at dusk. Approximately 50 nests were within the camera field in 1978 and about 40 in 1979. Since the blind housing the camera was farther from the study area in 1979 than in 1978, a zoom lens was used to produce similar sized camera fields for both years. Filming was almost continuous (diurnally, weather permitting) from 10 May to 5 July in 1978 and from 10 May to 16 July in 1979.

Film Analysis

A) Feeding rates 1978 versus 1979

Films were analyzed using multiple speed super-8 projectors equipped with a frame counter. Based on film clarity, three nests each year were chosen from nests within the camera field in which both A and B-chicks survived until at least B-chick 4 days. Films were analyzed for each of

these nests to determine the potential feeding rates from dawn of the B-chick hatch date until dusk three days later. The total time of undisturbed nest filming was measured in frames and each parental arrival at the nest was reviewed at slow projection speeds (two to seven frames per second) to determine whether or not a feeding potentially occurred. A potential feeding was scored if the incoming parent was seen to have a fish, or if that parent positioned and/or postured itself in a manner suggesting a feeding attempt.

B) Agents of Chick Disappearance

In an attempt to identify agents of chick disappearance, nests in which chicks disappeared, were reviewed for the period between the last nest check record of the chick and the next nest check (when that chick was first missed). The presence of hetero^specific intruders was noted along with parental behavior.

Statistical Analysts

Siegel (1956), Malec (1976) and Ryan et al. (1976) were used as references throughout data analyses. Tests of reproductive parameters were chi squared tests with Yate's correction for continuity (X_c^2) or the Fisher exact probability test (Siegal 1956). The organization of data and most other statistical tests were done using the Minitab Statistical Computing System (Ryan et al. 1976). Data which were naturally paired (i.e., A versus B-chicks in the same brood) were tested using a paired T-test (Ryan et al. 1976). Data not naturally paired were tested using a Wilcoxon Rank Sum Test (Ryan et al. 1976). These and other tests are specified, when used, in the text and tables.

RESULTS

Nest Checks

The first nest checks, both years, occurred prior to the first clutch initiation of the year by Caspian Terns. Recorded time spent in the colony during nest checks averaged 57.8 ± 7.43 minutes in 1978, and 70.1 ± 5.14 minutes in 1979.

Clutch Initiation and Sizes

In 1978, a peak in clutch initiations (67%, n=122) occurred between 9-15 May (Fig 2). Most clutches (87.4%, n=159) were initiated between 7-21 May whereas after 21 May, clutch initiations were infrequent. Accordingly, clutches initiated between 7-21 May were taken as the study sample for 1978. In 1979, a peak in clutch initiations (72.9%, n=89). occurred between 19-31 May (Fig 3). Most clutches (86.8%, n=106) were initiated between 9-31 May. After this period, clutches were initiated infrequently. Clutches initiated between 9-31 May were taken as the study sample for 1979.

Weather conditions during initiation of study nests are in Table 1. Generally, winds were stronger, and temperatures higher in 1978 compared with 1979.

The total number of clutches initiated on the north-east knoll (including non-study nests) by 21 May 1978 was 233. Of these, 50 nests lost all eggs by 21 May. The total number of clutches initiated on the north-west knoll by 28 June 1978 was 229, however, accurate records of egg losses were not kept. The total number of clutches initiated on the north-east knoll (including non-study nests) by 31 May 1979 was 201, of which 17 lost all eggs by 31 May. The total number of clutches initiated

Figure 2

The clutch initiation[1] distribution of the 1978 study area. The total number of clutches was 182.

[1] New nests were not sought during every nest check after 21 May.

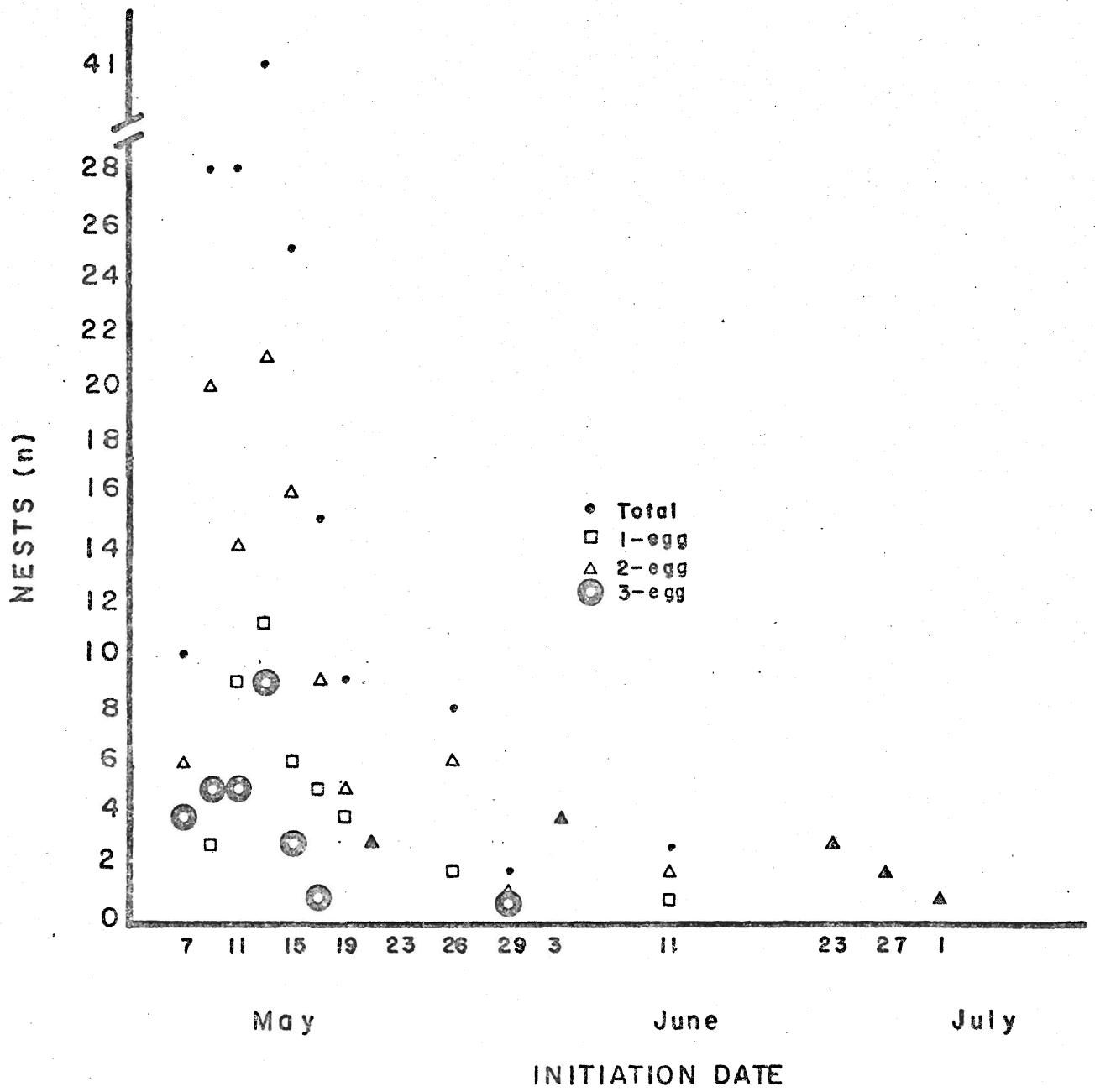

NESTS (n)
41
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
Total
1-egg
2-egg
3-egg
7
11
15
19
23
26
29
3
11
23
27
1
May
June
July
INITIATION DATE

Figure 3

The clutch initiation distribution of the 1979 study area. The total number of clutches was 122.

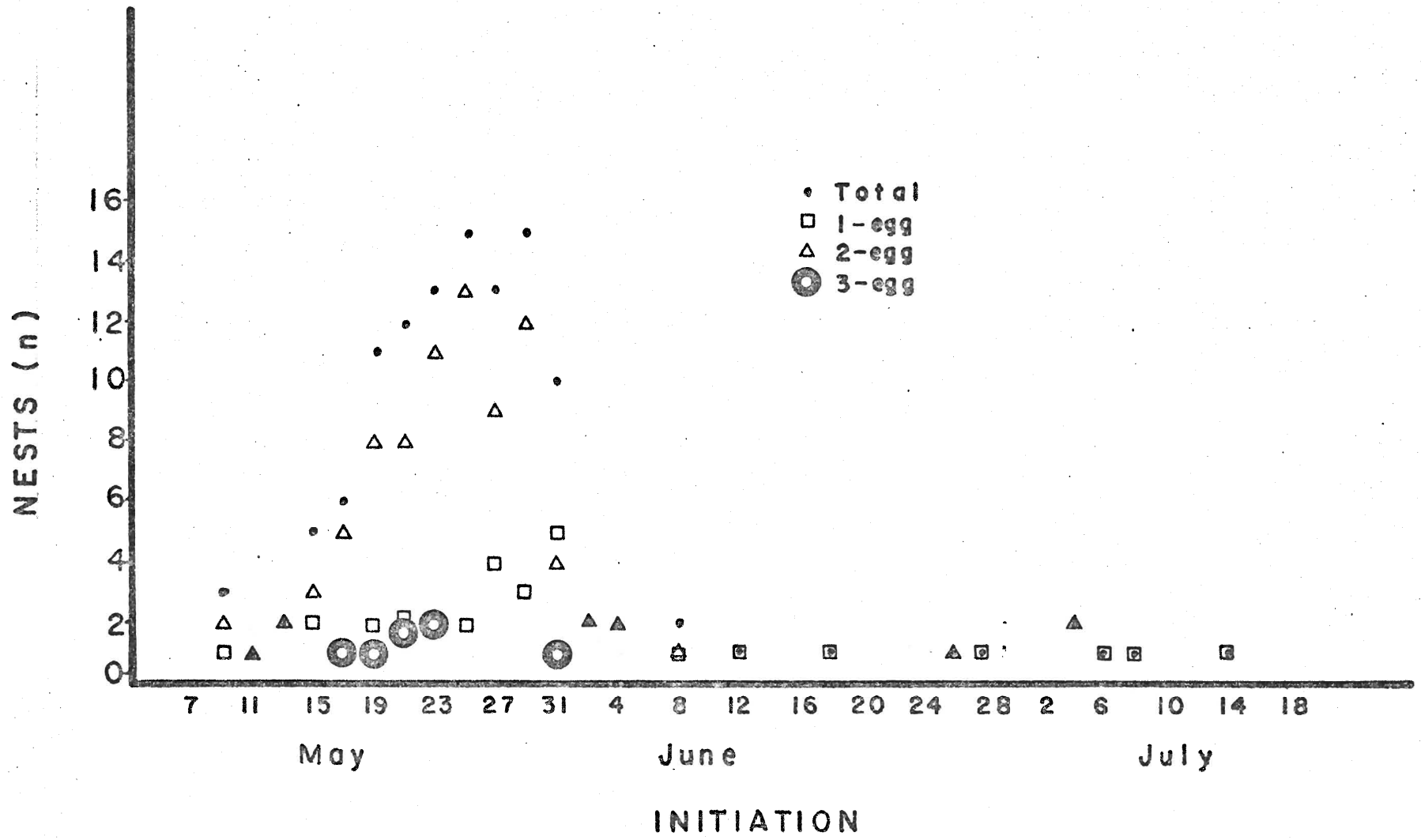

NESTS (n)
0
2
4
6
8
10
12
14
16
7
11
15
19
23
27
31
4
8
12
16
20
24
28
2
6
10
14
18
May
June
July
INITIATION
Total
1-egg
2-egg
3-egg

Table 1: Windspeed and Temperature during Clutch Initiation

	$\bar{x}$ Windspeed[1] ± Standard Error (km/hr)	$\bar{x}$ Daily Maximum[1] Windspeed ± Standard error (km/hr)	$\bar{x}$ Temperature ± Standard Error (°C)
1978 (7 to 21 May)	17.53 ± 1.907	31.133 ± 2.605	11.793 ± 0.764
1979 (9 to 31 May)	10.56 ± 1.22	21 ± 1.369	10.87 ± 0.786

[1]Based on Environment Canada Wind Summaries for Wiarton Ontario.

[2]Based on Environment Canada Monthly Climatological Summaries for Wiarton Ontario.

on the north-west knoll by 28 May was 147, however, as in 1978, accurate egg loss records were not kept.

The modal clutch size in both years was two eggs (Table 2). One-egg clutches were about as common both years (X_c^2) = 0.4, $P > 0.1$), however, 3-egg clutches were significantly more frequent in 1978 (X_c^2) = 5.23, $P < 0.05$).

There were no significant seasonal effects on hatching or fledging success of study nests initiated at different times (Appendix II).

The Eggs

Laying and Hatching Intervals and Incubation Time

A and B-eggs from 2-egg clutches which hatched both eggs were laid, on average, 2.7 ± 1.26 (n=50) days apart in 1978 and 2.3 ± 0.75 (n=54) days apart in 1979. In 1978 the incubation time for A-eggs (26.3 ± 1.30 days) was significantly longer than that of the B-eggs (25.1 ± 1.33 days; Paired T-test, $T = -5.691$, $n = 50$, $P < 0.0001$). In 1979, the incubation time for the A-eggs (26.3 ± 0.91 days) was significantly longer than that of the B-eggs (25.7 ± 0.90 days; Paired T-test, $T = -3.145$, $n = 54$, $P = 0.0027$). A and B-eggs from 2-egg clutches hatched, on average, 1.5 ± 0.89 days apart in 1978, and 1.8 ± 1.13 days apart in 1979. Eggs hatched in the same order as laid except in two 1979 clutches where the B-eggs hatched before the A-eggs. In these two cases, hatching order superceded laying order for analysis, therefore, these B-eggs were called and treated as A-eggs and *vice versa*. In 1978, 23.8% (n=15) of clutches hatching A and B-eggs hatched on the same interval between nest checks, whereas, 6.8% (n=4) did so in 1979.

Table 2: The Distribution of Clutch Sizes for 1978 and 1979 Study Areas

	CLUTCH SIZE			
	One-egg n (%)	Two-egg n (%)	Three-egg n (%)	Total
1978	38 (25%)	94 (59%)	27 (18%)	159
1979	21 (20%)	78 (74%)	7 (7%)	106

Egg Weights

The fresh weight of A-eggs in 2-egg clutches (69.9 ± 5.87 gms) was significantly greater than that of B-eggs (65.7 ± 7.91 gms; Paired T-Test, $T = 3.712$, $n = 47$, $P = 0.0006$). The fresh weight of eggs tended to decline with later clutch initiation dates. The trend was significant for B-eggs (Spearman Rank Correlation, $rs = -0.298$, $n = 51$, $P < 0.05$) but not for A-eggs (Spearman Rank Correlation, $rs = -0.246$, $n = 53$, $P > 0.05$).

A-egg weights correlated significantly with the weights of their B-egg siblings (Spearman Rank Correlation, $rs = +0.597$, $n = 47$, $P < 0.01$). The difference in fresh weights between A and B-eggs correlated significantly with A-egg weight (Spearman Rank Correlation, $rs = +0.577$, $n = 47$, $P < 0.01$). No significant correlation was found for B-egg weight (Spearman Tank Correlation $rs = -0.24$, $n = 47$, $P > 0.05$) or total clutch weight (Spearman Rank Correlation $rs = +0.183$, $n = 47$, $P > 0.05$).

The mean weight of four adult Caspian Terns (sex unknown) captured on eggs in Lavaca Bay, Texas, during late June and early May of 1980 was 731.7 ± 15.84 gms. Assuming this weight approximates that of female Caspian Terns nesting on South Limestone Island during 1979, A-eggs represented about 9.55% of the females' body weight while B-eggs represented about 8.98%.

Hatching Success

Eggs which hatched from 2-egg clutches had similar fresh weights to those which did not (A-eggs, Wilcoxon Rank Sum Test, $W1 = 1647.5$, $W2 = 980.5$, $n1 = 44$, $n2 = 28$, $P = 0.6358$; B-eggs, $W1 = 1196.0$, $W2 = 344.0$, $n1 = 42$, $n2 = 13$, $P = 0.6993$). The fates of A and B-eggs in 2-egg clutches were similar both years (Table 2). Hatching success rates of A and B-eggs were similar in 1978 ($\chi^2_c = 0$, $P > 0.1$) and in 1979

($X^2_c = 0.116$, $P > 0.1$). Hatching success rates of B and C-eggs of 3-egg clutches were not significantly different in 1978 ($X^2_c = 1.1689$, $P > 0.1$) or in 1979 (Fisher Exact Probability Test, $P = 0.367$).

The hatching success of 2-egg clutches was significantly greater in 1979 than 1978 ($X^2_c = 8.48$, $P < 0.01$). This difference was a result of higher frequencies of disappeared and destroyed eggs in 1978 (Table 3).

The Chicks

The dyeing schedule used to differentiate chicks within broods had no apparent effect on chick-chick or parent-chick interactions, either year.

Foraging and Chick Feeding

Most foraging went on out of sight from the island chain. Foraging parents flew off in the general direction of the mainland and returned from the same general direction. Occasionally adults foraged for Ninespine Sticklebacks (Pungitius pungitius) in a shallow bay between the islands, especially early in the chick feeding period. Prey items were carried individually to the nest in the bill. Chicks were fed whole fish which they swallowed head-first. Chick feedings rarely involved sibling aggression and such aggression, when it occurred, did not cause any apparent injury. Chicks became increasingly mobile after age 5 days and would approach unrelated adults which were carrying fish. Conspecific kleptoparasitism was observed at the colony.

Chick begging involved begging calls and a scissoring of the parent's bill tip by the chick. Begging occurred throughout the day, especially after a parent returned to its nest without a fish.

Table 3: Egg Fates of A and B-Eggs from Two-Egg Clutches (1978 and 1979)

Year	Laying Order	Total Laid	Hatched	Disappeared	Destroyed[1]	Addled[2]	Died While Pipping	Cracked	Rolled Out	Failed to Hatch	Worker[3] Error
1978	A	94	59(63%)	19(20%)	11(19%)	3(3%)	0(0%)	1(1%)	1(1%)	0(0%)	0(0%)
	B	94	58(62%)	21(22%)	8(9%)	3(3%)	2(2%)	0(0%)	1(1%)	0(0%)	1(1%)
1979	A	78	59(76%)	6(8%)	5(6%)	3(3%)	1(1%)	2(3%)	1(1%)	0(0%)	1(1%)
	B[4]	77	61(79%)	3(4%)	4(5%)	5(6%)	1(1%)	1(1%)	0(0%)	2(3%)	0(0%)

[1]Egg found with small hole or smashed open during nest check, or was observed being broken and/or eaten by Ring-billed Gulls during blind observations.

[2]Egg remained intact for 30 days or more without hatching (in the nest), or exhibited a liquid center.

[3]Two eggs were broken by research workers.

[4]One egg fate was not recorded (did not hatch).

Prey Species Identification and Chick Feeding

Chick feeding data were based on 157.5 hours of observation in 1978 and 165 hours in 1979. Species of fish identified as prey species were Alewife (Alosa pseudoharengus), Emerald Shiner (Notropis antherinoides), Northern Pike (Esox lucius), Ninespine Stickleback, Pumpkinseed (Lepomis gibbosus), Rainbow Smelt (Osmerus mordax), Rock Bass (Ambloplites rupestris), Smallmouth Bass (Micropterus dolomieue), and Yellow Perch (Perca flavescens). On single occasions unidentified species of sucker and catfish (or bullhead) were fed to chicks. Three species of fish which were fed infrequently were unknown. The proportions of fish species fed to chicks, according to chick age, are in Figure 4. Rainbow Smelt was the major food type fed to chicks until age 12 days. After this age the proportion of Rainbow Smelt fed to chicks declined as the proportion of Rock Bass increased (Fig 4). Rainbow Smelt was an important food fed to chicks early in the season (especially until about 22 June; Figs 5, 6). Rock Bass were fed relatively frequently between 22 and 30 June, after which no Rock Bass were recorded during chick feeding observations (Figs 5, 6).

Mean estimated prey weights were determined as a function of chick age, both years (Fig 7). These mean weights tended to increase with chick age over the first 15 days.

During 1978, 83.3% (n = 414) of the feedings to chicks in study nests (remaining feeding data refer only to study nests) allowed weight assignments using prey species length-weight curves (Appendix Table I). In 14.3% (n = 71) of the feedings, the length and/or prey speeies (or body shape) was not determined. In 2.4% (n = 12) feedings, the identity of the chick fed was unknown.

Figure 4

Food type variation during combined morning and evening observation periods against chick age, in 1978[1][2][3]

[1] The frequency of each major food type is expressed as a percentage of total food types fed to chicks of the designated age during observation periods from 6 June to 5 August 1978, including all feedings observed (not just study nests).

[2] The total number of feedings observed to chicks of each age is above the bar for that age.

[3] The total number of feedings varied for the various ages because of differences in the number of chicks observed, the weather, and the number of hours the age class was observed.

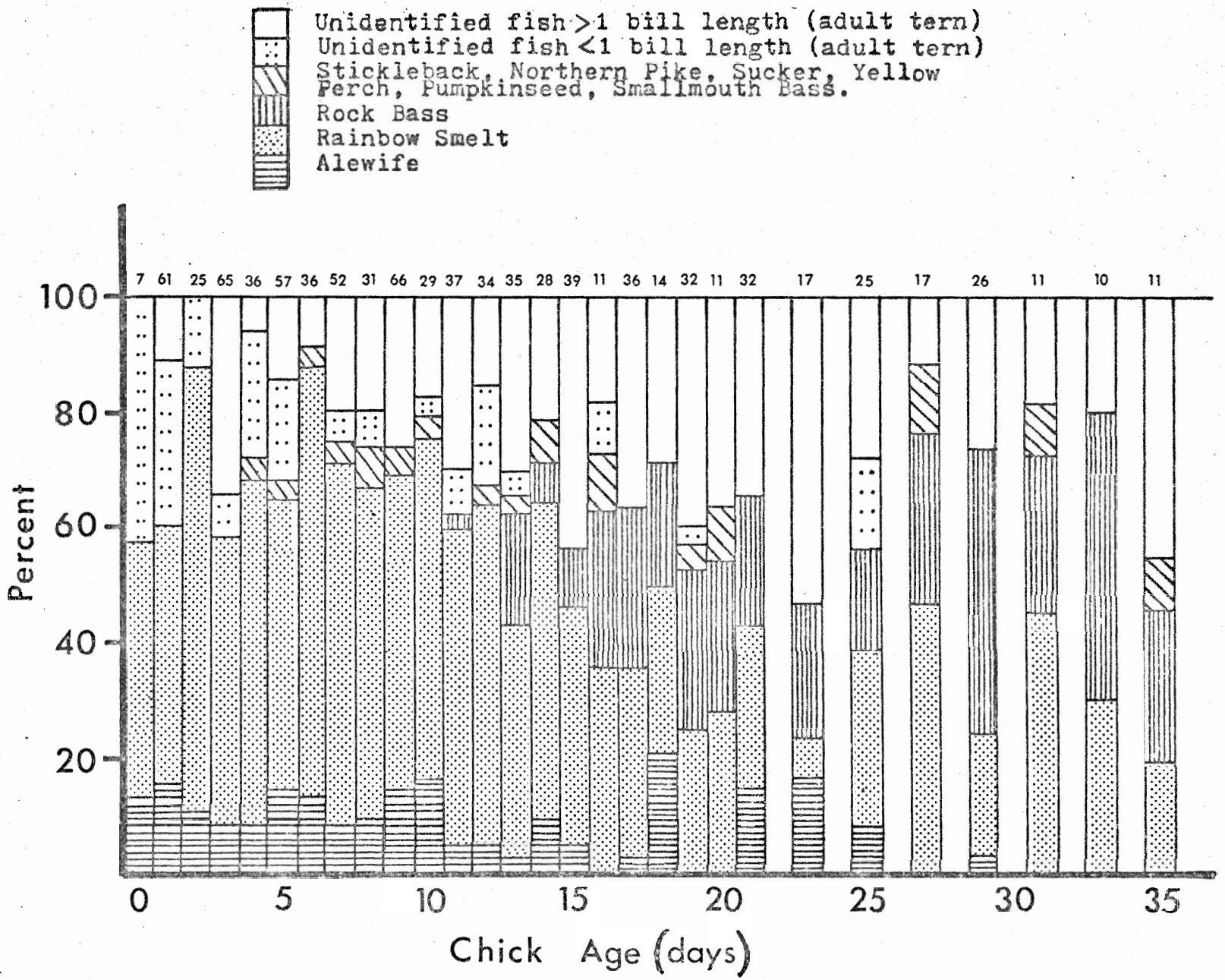

Unidentified fish >1 bill length (adult tern)
Unidentified fish <1 bill length (adult tern)
Stickleback, Northern Pike, Sucker, Yellow Perch, Pumpkinseed, Smallmouth Bass.
Rock Bass
Rainbow Smelt
Alewife
7 61 25 65 36 57 36 52 31 66 29 37 34 35 28 39 11 36 14 32 11 32 17 25 17 26 11 10 11
100
80
60
40
20
Percent
0
5
10
15
20
25
30
35
Chick Age (days)

Figure 5

Food type[1] variation during morning observation periods (07:30 - 10:00) against time of season,[2] in 1978.

[1] The frequency of each major food type is expressed as a percentage of total food types fed during observation periods from 4 June to 11 August, including all feedings observed (not just study nests).

[2] The total number of feedings observed on each day is above the bar for that day.

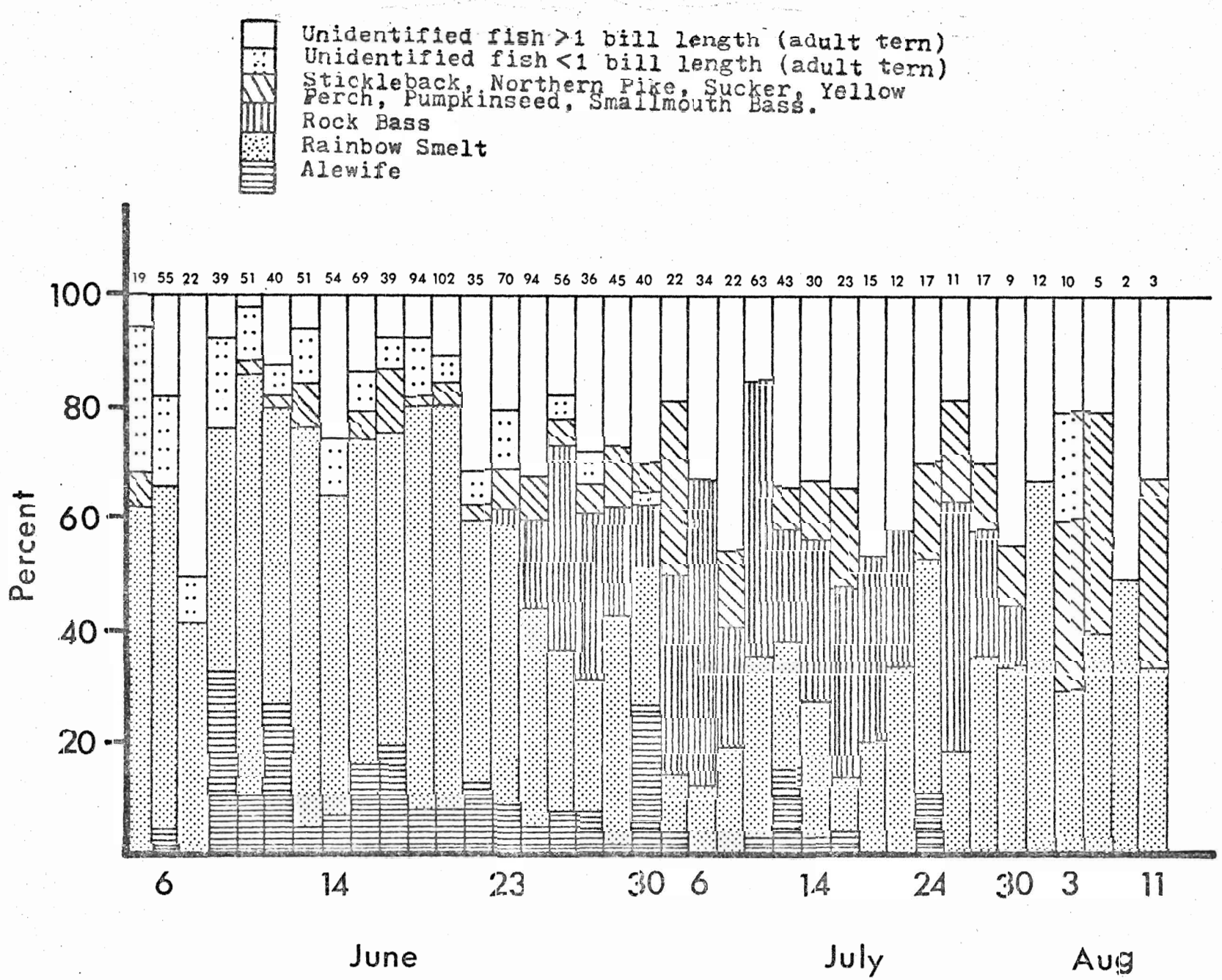

Unidentified fish >1 bill length (adult tern)
Unidentified fish <1 bill length (adult tern)
Stickleback, Northern Pike, Sucker, Yellow Perch, Pumpkinseed, Smallmouth Bass.
Rock Bass
Rainbow Smelt
Alewife
19 55 22 39 51 40 51 54 69 39 94 102 35 70 94 56 36 45 40 22 34 22 63 43 30 23 15 12 17 11 17 9 12 10 5 2 3
100
80
60
40
20
Percent
6
14
23
30
6
14
24
30
3
11
June
July
Aug

Figure 6

Food type[1] variation during evening observation periods (18:30 - 21:00) against time of season[2] in 1978

1 The frequency of each major food type is expressed as a percentage of total food types fed during observation periods from 6 June to 5 August, including all feedings observed (not just study nests).

2 The total number of feedings observed on each day is above the bar for that day.

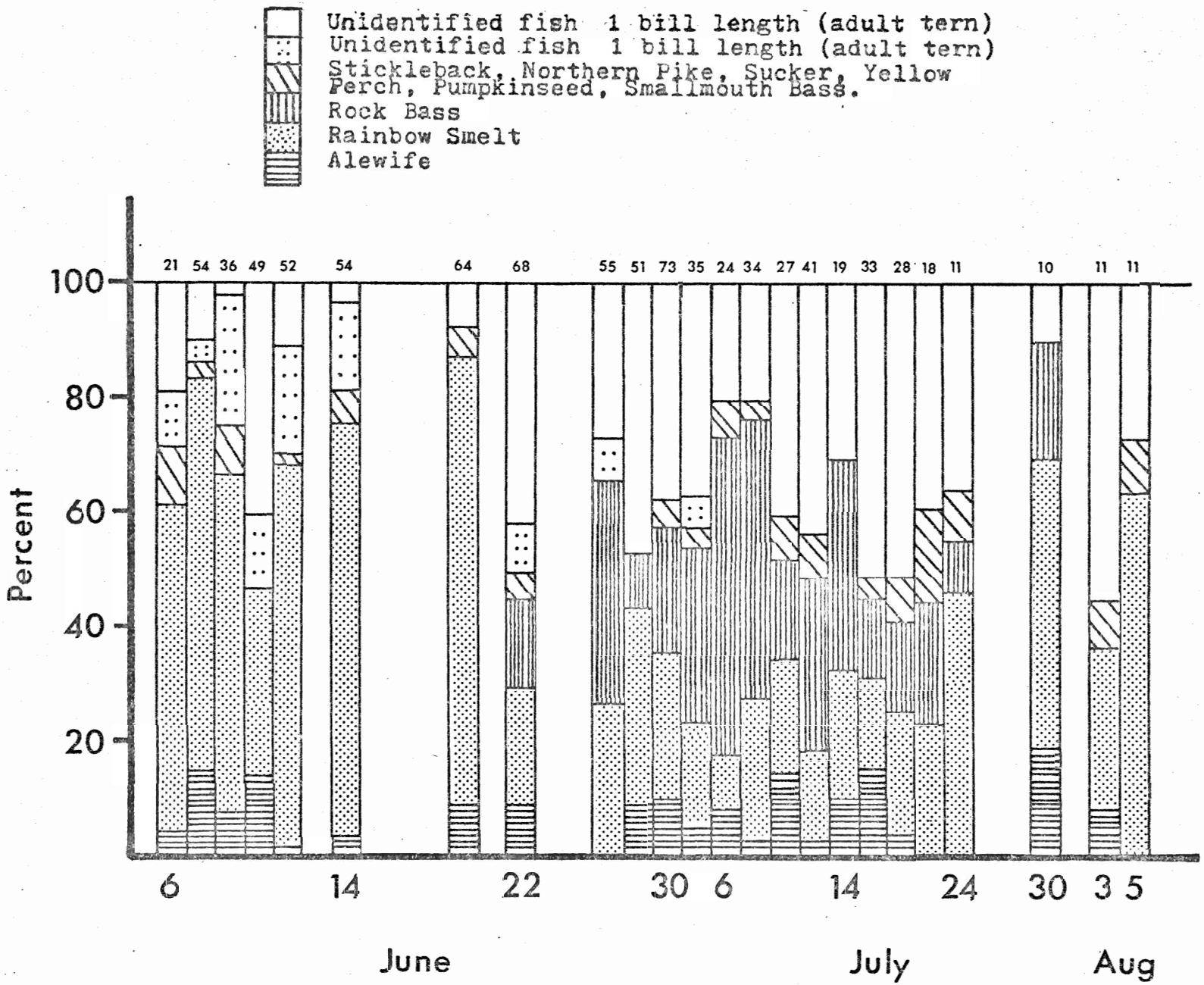
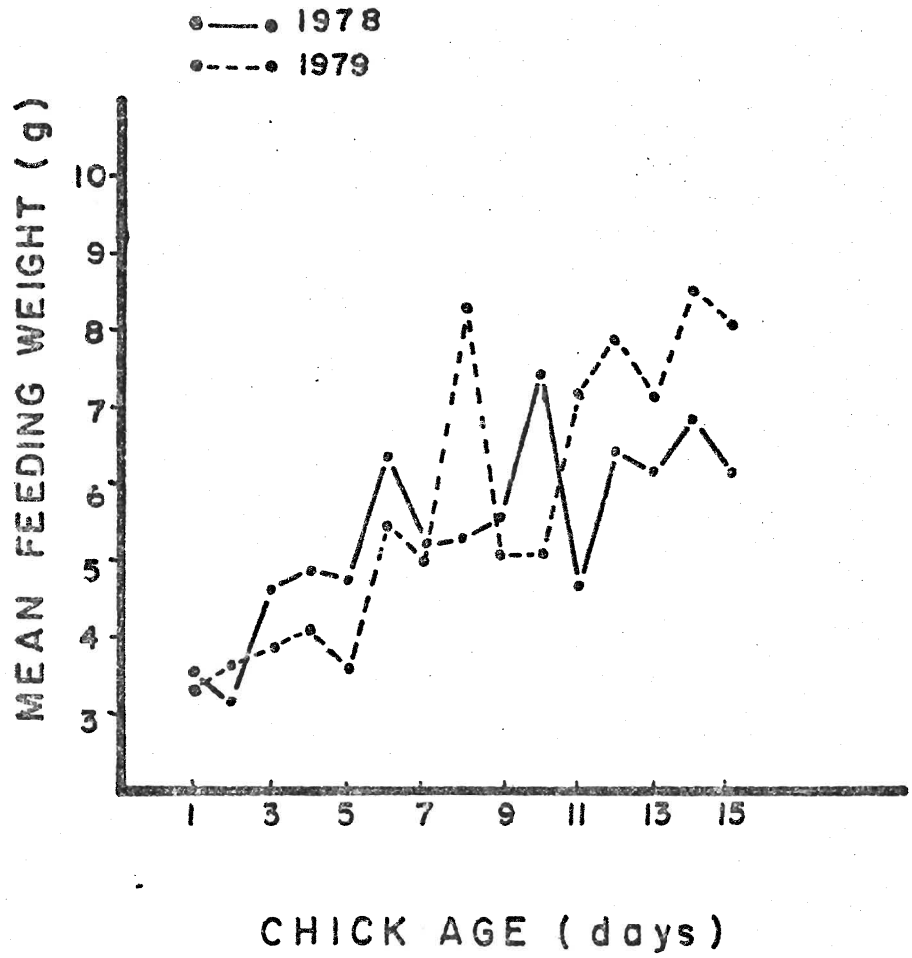

Unidentified fish 1 bill length (adult tern)
Unidentified fish 1 bill length (adult tern)
Stickleback, Northern Pike, Sucker, Yellow Perch, Pumpkinseed, Smallmouth Bass.
Rock Bass
Rainbow Smelt
Alewife
Percent
100
80
60
40
20
21 54 36 49 52 54 64 68 55 51 73 35 24 34 27 41 19 33 28 18 11 10 11 11
6 14 22 30 6 14 24 30 3 5
June
July
Aug

Figure 7

Mean estimated weight[1] of prey items fed to chicks in study nests[2] according to chick age, 1978 and 1979

[1] Including only weights estimated directly from length-weight curves.

[2] Feedings to chicks in study nests were included for the first 15 days, both before and after the loss of a sibling (if a sibling was lost).


1978
1979
MEAN FEEDING WEIGHT (g)
10
9
8
7
6
5
4
3
1
3
5
7
9
11
13
15
CHICK AGE (days)

In 1979, 80% (n=175) of the feeding included in this study allowed weight assignment using length weight curve. In 6.9% (n=15) of the feedings, lengths were observed but species (or body shape) identifications were not made. In 7.3% (n=16) of the feedings, neither the species (or body shape) nor length were known. In 5.5% (n=12) of the feedings, the identity of the chick fed was unknown.

Film Analysis of Feeding Visitation Rates

Film analyses of three nests in each year were used to estimate feeding rates to 2-chick broods from B-chick hatching to 3 days of B-chick's age (Table 4). Nests were chosen each year based on brood survival through the period analyzed and on clarity of the film record. Weather conditions during the periods analyzed were similar, excepting some between year differences in total percipitation (Table 5). Estimated maximum feeding rates were higher in 1978 than 1979 (Mann Whitney U Test, $U = 0$, $n_1 = 3$, $n_2 = 3$, $P = 0.05$).

Feeding Rates to A and B-Chicks

Chicks from 2 and 3-egg clutches had similar feeding rates and within brood food apportionment (Table 6). Accordingly, feeding rates reported below were based on chicks from 2 and 3-egg clutches. Feeding rates were determined as a function of B-chick age, thus ages reported are those of B-chicks.

Feeding rates were determined for broods with both A and B-chicks alive (Figs 8, 9). In 1978, A-chicks generally were fed at a higher rate than B-chicks, however, based on 95% confidence intervals, the differences were significant only at ages 0-1, 6-7, and 8-9 days (Fig 8). The disparity in feeding rates between A and B-chicks was

Table 4: Estimated Feeding Rates to Three Broods in Each of the Two Years as Determined from Film Analysis. The rates relate to estimated maximum feeding visits to the broods between the B-chicks' ages of 0-3 days.

Year	Nest Number	Total[1] Feedings (n)	Total Frames (n)	Total Standardized[2] Frames	Feeding Rate[1] Feedings per Standardized Frame
1978	116	31	17404	16979	1.82×10^{-3}
	105	17	17404	16979	1×10^{-3}
	111	22	17336	16913	1.3×10^{-3}
1979	207	14	19205	19205	7.29×10^{-4}
	113	11	20331	20331	5.41×10^{-4}
	130	12	18782	18782	6.39×10^{-4}

[1]Actual feedings could not be discerned from films, therefore, these are estimated maximum feeding rates.

[2]In order to adjust for slight filmspeed differences between years, 1978 total frame numbers were multiplied by a correction factor of 0.9756 as determined by film speed comparisons.

Table 5: Weather Conditions[1] at Wiarton during the Filming of Nests in Table 4

Year	Nest Number	Dates Analyzed Day/Month	$\bar{X}$ Temperature over Period (°C)	Total Precipitation over Period (mm)	Number of Days with Some Fog	Windspeed: Mean of Daily Means over Period (km/hr)	Windspeed: Mean of Daily Maximum over Period (km/hr)
	116	10/6-13/6	14.85	18.6	0	19.3	32.75
1978	105	10/6-13/6	14.85	18.6	0	19.3	32.75
	111	8/6-11/6	13.87	30.0	1	16.5	29.5
	207	21/6-24/6	12.5	2.6	0	15.1	29.5
1979	113	13/6-16/6	17.55	8.0	0	18.5	31.5
	130	19/6-22/6	16.85	1.4	0	16.57	32.25

[1]Obtained from Environment Canada (Canadian Climate Center).

Table 6: Wilcoxon Rank Sum Comparisons of Feeding Rates to Broods, and Intra-brood Food Apportionment between Broods from 2 versus 3-egg Clutches in 1978

Comparison	B-chick Age Period (days)	W1	W2	n1	n2	P
Feeding Rates	0-5	95.5	40.5	11	5	0.865
	6-10	151.5	38.5	15	4	0.920
	11-15	109.5	26.5	12	4	0.396
Intra-brood[1] Apportionment	0-5	85.5	49.5	11	5	0.461
	6-10	146.5	43.5	15	4	0.764
	11-15	114.5	21.5	12	4	0.146

[1]Intra-brood apportionment is tested using the % of total food brought to the nest during the period that was fed to the B-chick. C-chicks were observed being fed only twice.

Figure 8

The relationship between mean feeding rates[1] and chick age[2] for A and B-chicks[3] from 1978[4]

[1] Means are shown with 95% confidence intervals with the number of 30 minute sampling periods and the number of broods observed shown.

[2] B-chick age for each brood.

[3] Means are based on feeding rates to chicks of broods with A and B-chicks alive from 2 and 3-egg clutches.

[4] Observation techniques differed between 1978 and 1979 and 1979 feeding rates are inflated relative to 1978 rates

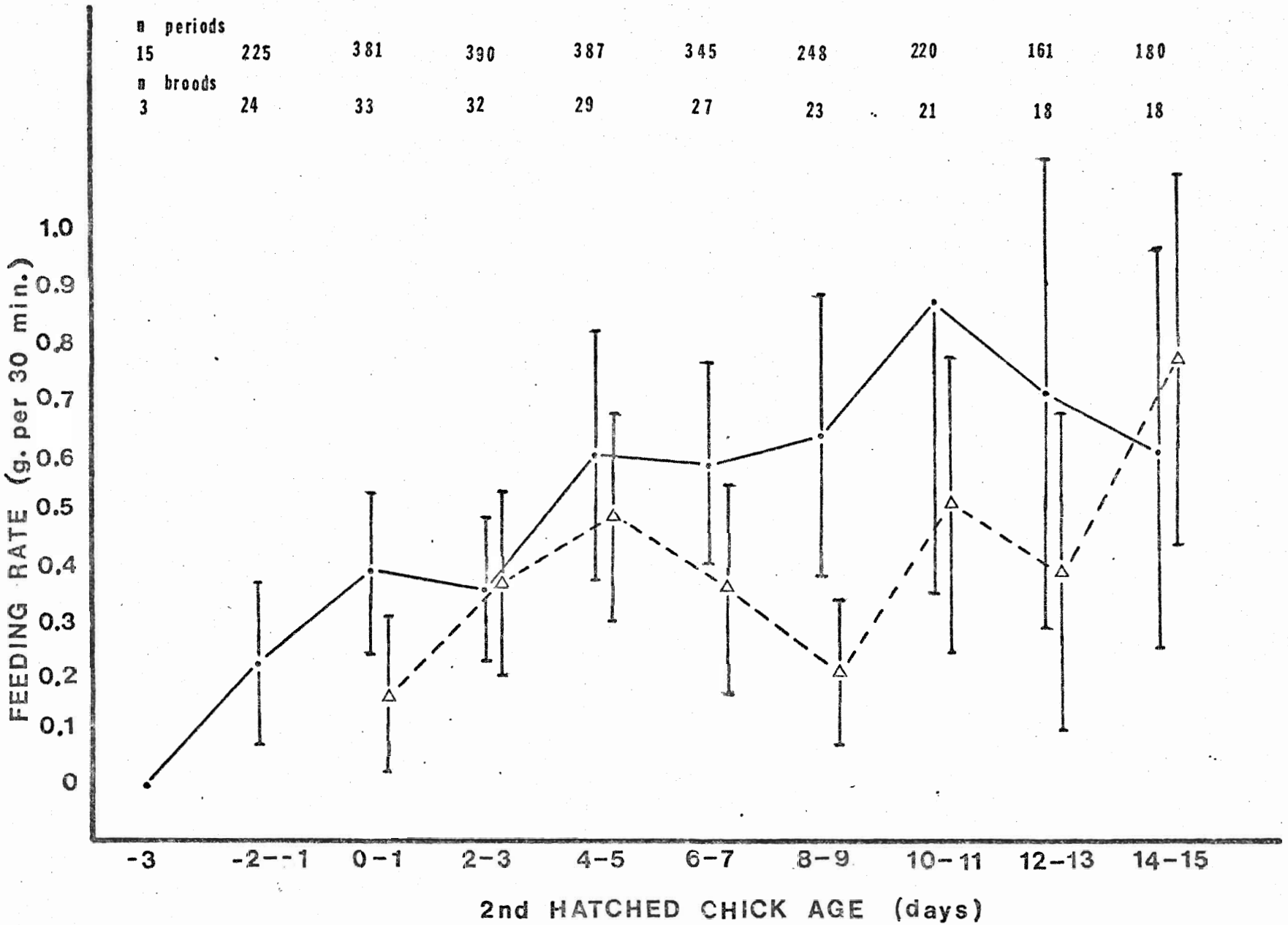

n periods
15 225 381 390 387 345 248 220 161 180
n broods
3 24 33 32 29 27 23 21 18 18
FEEDING RATE (g. per 30 min.)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-3
-2--1
0-1
2-3
4-5
6-7
8-9
10-11
12-13
14-15
2nd HATCHED CHICK AGE (days)

Figure 9

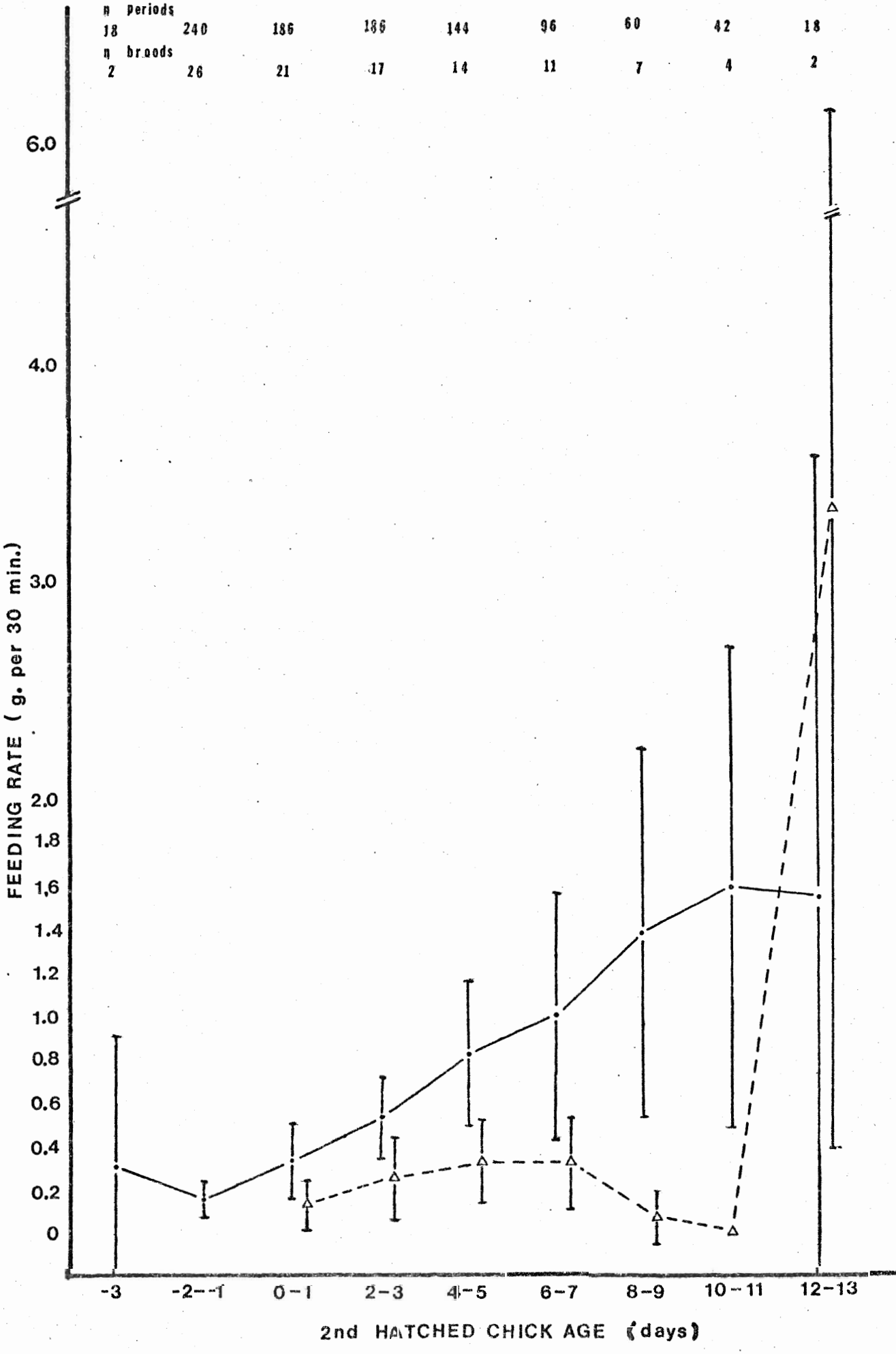
The relationship between mean feeding rates[1] and chick age[2] for A and B-chicks[3] from 1979[4]

[1] Means are shown with 95% confidence intervals with the number of 30 minute sampling periods, and the number of broods observed, shown.

[2] B-chick age for each brood.

[3] Means were based on feeding rates to chicks of broods with A and B-chicks alive, from 2 and 3-egg clutches.

[4] Observation techniques differed between 1978 and 1979 and 1979 feeding rates are inflated relative to 1978 rates.


n periods
18 240 186 186 144 96 60 42 18
n broods
2 26 21 17 14 11 7 4 2
6.0
4.0
3.0
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
FEEDING RATE (g. per 30 min.)
-3
-2--1
0-1
2-3
4-5
6-7
8-9
10-11
12-13
2nd HATCHED CHICK AGE (days)

greater in 1979 (Fig 9). A-chicks were fed at a significantly greater rate than B-chicks at ages 0-11 days (Fig 9). Feeding rates at ages 12-13 days were based on two broods, and one was the only 1979 brood to raise two chicks to a flying stage (Fig 9). Despite more efficient observation techniques used in 1979, B-chicks from ages 0-13 days were fed at a greater overall rate in 1978 than 1979. The weighted mean (weighted for number of chicks observed at each age) feeding rate for 0-13 day old B-chicks in 1978 was 0.346 grams per 30 minutes while the corresponding value for 1979 was 0.288 grams per 30 minutes.

Feeding Rates According to Ages and Fates of B-Chicks

For clarity, broods with different B-chick fates were classified into specific categories. Broods with B-chicks that survived through 15 days post-hatch (at least) were called brood category 1 (survived). Similarly, broods with B-chicks that died or disappeared were called brood category 2 (died) and brood category 3 (disappeared), respectively. By considering feeding rates to chicks included in specific brood categories, sample sizes were reduced and confidence intervals increased. Because of large confidence intervals, I treated these data as trends in the following manner. Feeding rate comparisons between and within brood categories were based on standard error bar overlap. When standard error bars of two mean feeding rates overlapped, they were considered similar. If they did not, they were considered different.

Feeding rates to members of specific brood categories from 1978 are shown for A-chicks (Fig 10) and B-chicks (Fig 11). A-chicks of brood category 2 (died; recall, this refers to the B-chick fate) were fed at a lower rate than A-chicks of brood category 3 (disappeared) at ages 8-9

Figure 10

The relationship between feeding rate[1] and chick age[2] for A-chicks[3] of broods in which the B-chick survived at least 15 days post hatch, the B-chick died within 15 days of hatching, or the B-chick disappeared within 15 days of hatching, from 1978

1 Means are shown with standard errors. The number of 30-minute sampling periods and the number of broods observed can be attained from the corresponding figures (Figs 12, 13, 14).

2 B-chick age for each brood.

3 Means are based on feeding rates to chicks of broods with A and B-chicks alive, from 2 and 3-egg hatches.

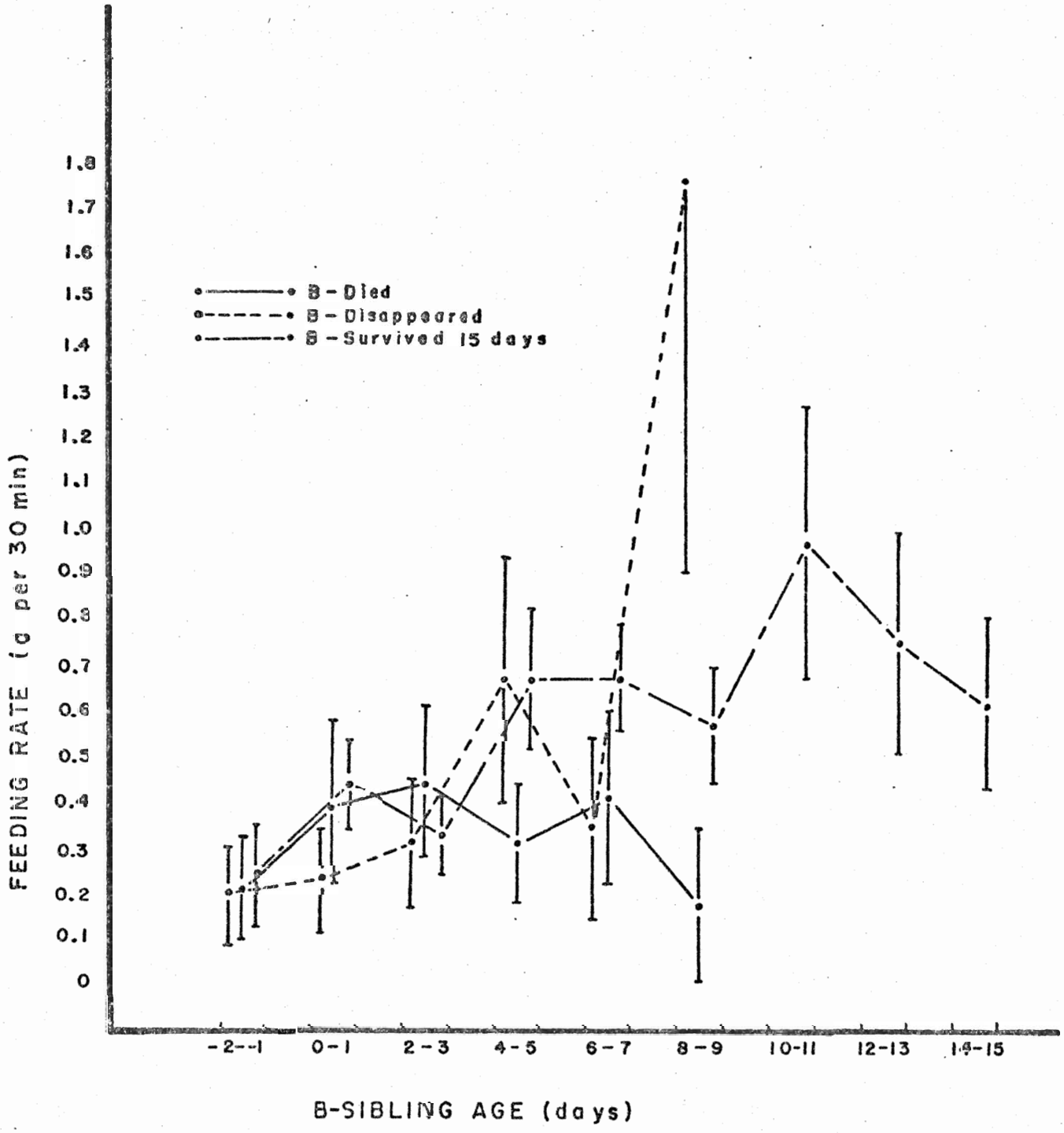

B - Died
B - Disappeared
B - Survived 15 days
FEEDING RATE (α per 30 min)
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-2--1
0-1
2-3
4-5
6-7
8-9
10-11
12-13
14-15
B-SIBLING AGE (days)

Figure 11

The relationship between feeding rate[1] and chick age[2] for B-chicks[3] of broods in which the B-chick survived at least 15 days post hatch, the B-chick died within 15 days of hatching, or the B-chick disappeared within 15 days of hatching, from 1978

1 Means are shown with standard errors. The number of 30 minute sampling periods and the number of broods observed can be attained from the corresponding figures (Figs 12, 13, 14).

2 B-chick age for each brood.

3 Means are based on feeding rates to chicks of broods with A and B-chicks alive, from 2 and 3-egg clutches.

FEEDING RATE (g per 30 min)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
B-CHICK AGE (days)
0-1
2-3
4-5
6-7
8-9
10-11
12-13
14-15
B Died
B Disappeared
B Survived 15 days

days (recall, these are B-chick ages) and at a lower rate than A-chicks of brood category 1 (survived) at ages 4-5 and 8-9 days (Fig 10). A-chicks of brood category 1 (survived) were fed at a greater rate than those of brood category 3 (disappeared) at ages 6-7 days, and at a slower rate than A-chicks of brood category 3 (disappeared) at ages 8-9 days (Fig 10). B-chicks of brood category 2 (died) were fed at a lower rate than those of brood category 3 (disappeared) at ages 8-9 days, and at a lower rate than B-chicks of brood category 1 (survived) at ages 4-5 and 8-9 days (Fig 11).

Feeding rates to A and B-chicks from 1978 are shown together, according to specific brood categories (Figs 12, 13, 14). A-chicks of brood category 1 (survived) were fed, in general, at a greater rate than their B-siblings, however, feeding rates were similar at ages 2-7 and 12-15 days (Fig 12). A and B-chicks of brood category 2 (died) were fed at similar rates at ages 2-9 days, but at 0-1 days, B-chicks were fed at a slower rate (Fig 13). A and B-chicks of brood category 3 (disappeared) were fed at similar rates from ages 0-9 days (Fig 14).

Feeding rates to members of specific brood categories from 1979 are shown for A-chicks (Fig 15) and B-chicks (Fig 16). A-chicks of brood category 3 (disappeared; recall, this refers to the B-chick fate) were fed at slower rates than A-chicks of brood category 1 (survived) at ages -2 to -1, 0-1, and 2-3 days (recall, these are B-chick ages; Fig 15). B-chicks of brood category 3 (disappeared) were fed at a slower rate than B-chicks of brood category 1 (survived) at ages 6-7 days, and at a slower rate than B-chicks of brood category 2 (died) at ages 2-3 and 8-9 days (Fig 16). B-chicks of brood category 2 (died) were fed at a slower rate than B-chicks of brood category 1 (survived)

Figure 12

The relationship between mean feeding rates[1] and chick age[2] for A and B-chicks[3] of broods in which the B-chick survived at least 15 days post hatch, from 1978

[1] Means are shown with standard errors and the number of 30 minute sampling periods, and the number of broods observed.

[2] B-chick age for each brood.

[3] Means were based on feeding rates to chicks of broods with A and B-chicks alive from 2 and 3-egg clutches.

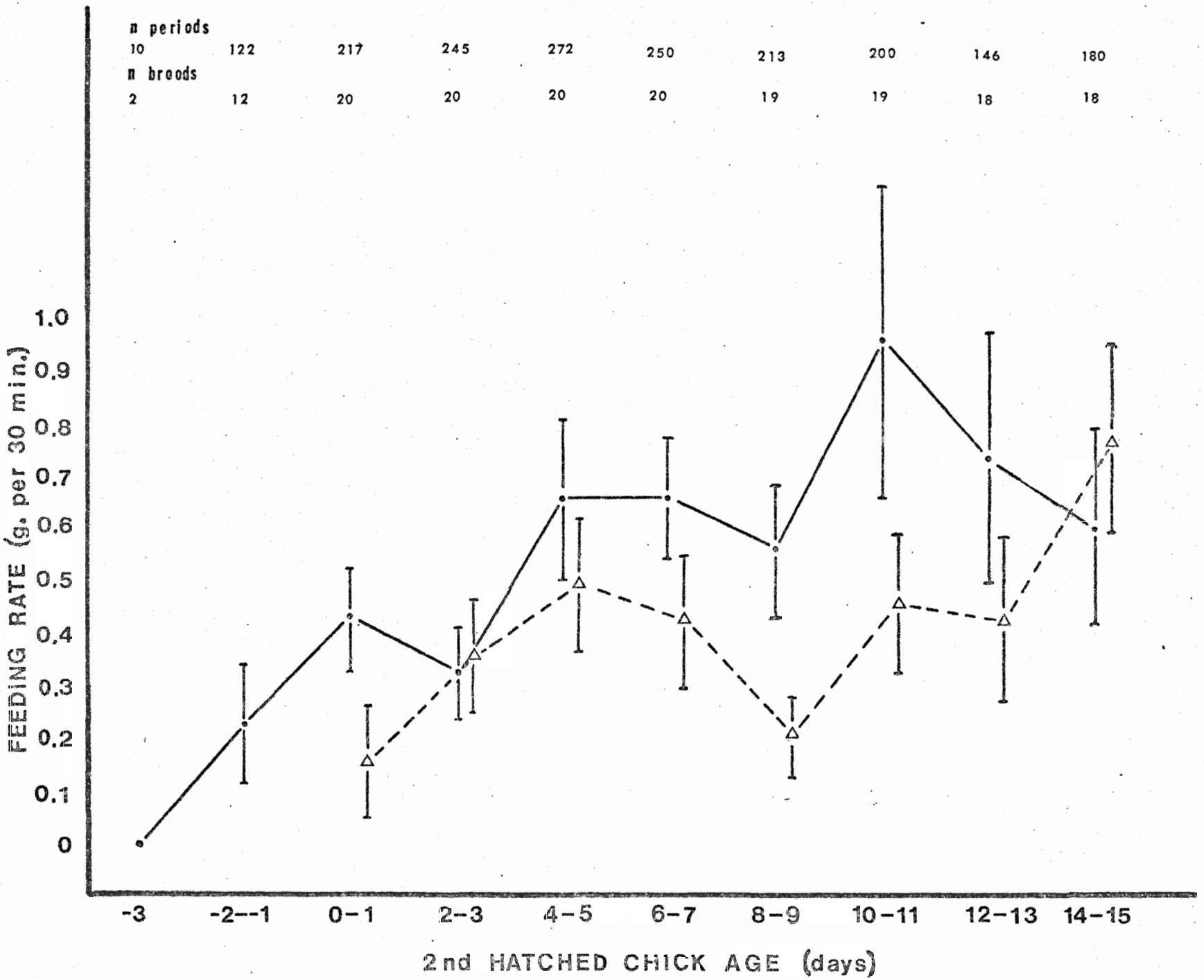

n periods
10 122 217 245 272 250 213 200 146 180
n broods
2 12 20 20 20 20 19 19 18 18
FEEDING RATE (g. per 30 min.)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-3
-2--1
0-1
2-3
4-5
6-7
8-9
10-11
12-13
14-15
2nd HATCHED CHICK AGE (days)

Figure 13

The relationship between mean feeding rates[1] and chick age[2] for A and B-chicks[3] of broods in which the B-chick died within 15 days of hatching, from 1978

[1] Means are shown with standard errors and the number of 30 minute sampling periods, and the number of broods observed. Means included are based on at least two broods.

[2] B-chick age for each brood.

[3] Means are based on feeding rates to chicks of broods with A and B-chicks alive, from 2 and 3-egg clutches.

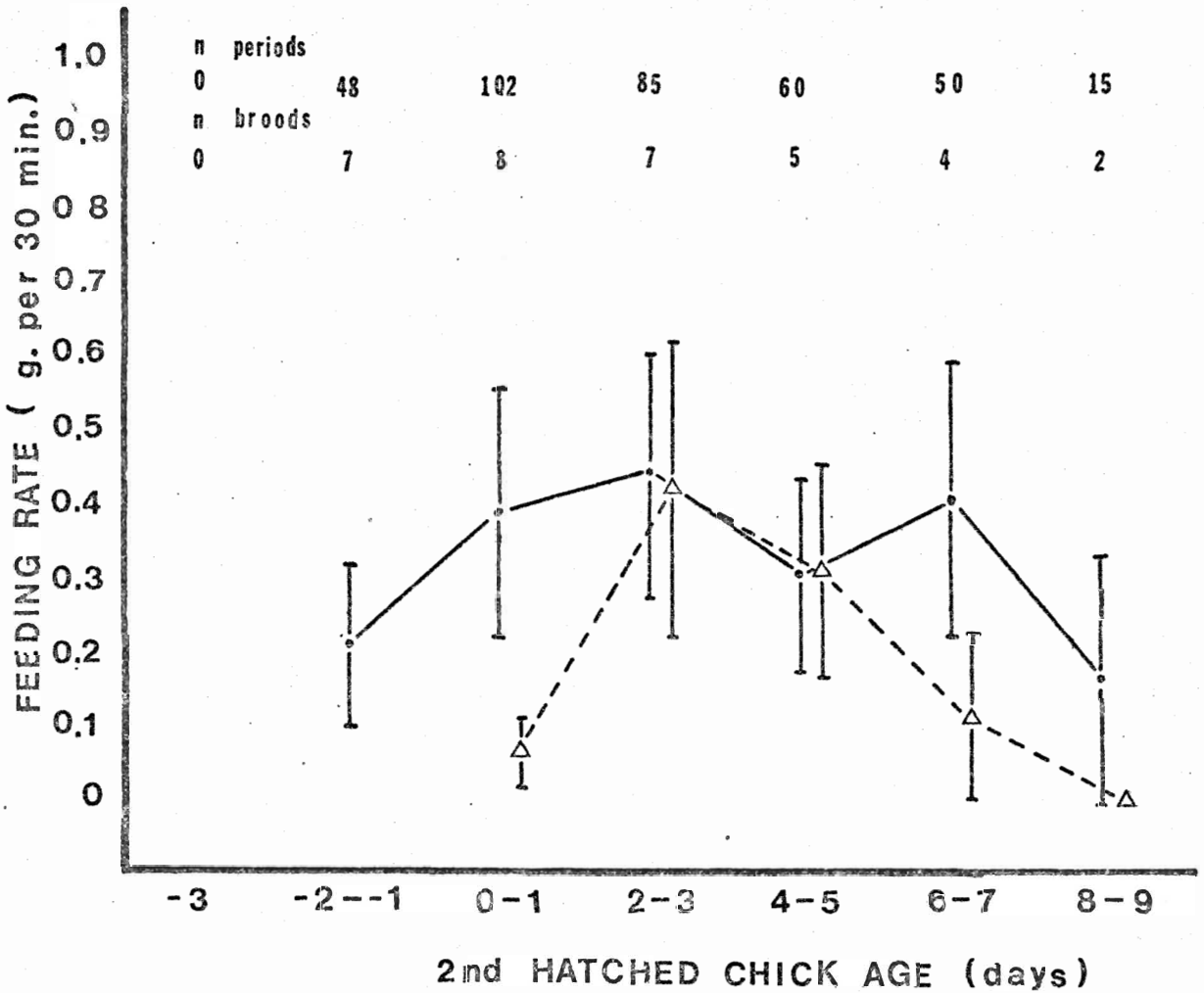

n periods
0
48
102
85
60
50
15
n broods
0
7
8
7
5
4
2
FEEDING RATE (g. per 30 min.)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-3
-2--1
0-1
2-3
4-5
6-7
8-9
2nd HATCHED CHICK AGE (days)

Figure 14

The relationship between mean feeding rates[1] and chick age[2] for A and B-chicks of broods in which the B-chick disappeared within 15 days of hatching, from 1978

[1] Means are shown with standard errors with the number of 30 minute sampling periods, and the number of broods observed. Means included are based on at least two broods.

[2] B-chick age for each brood

[3] Means are based on feeding rates to chicks of broods with A and B-chicks alive, from 2 and 3-egg clutches.

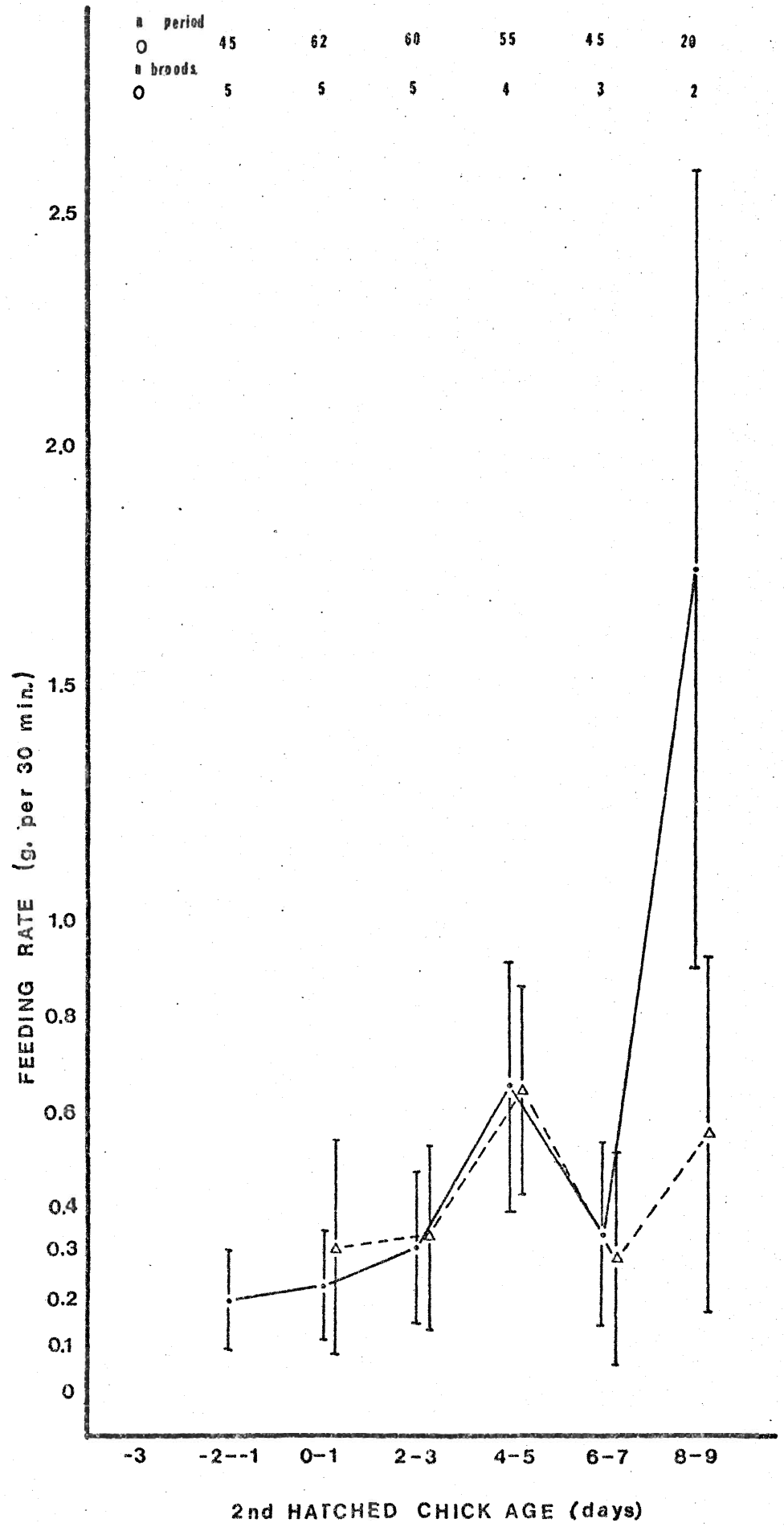

n period
45 62 60 55 45 20
n broods
5 5 5 4 3 2
2.5
2.0
1.5
1.0
0.8
0.6
0.4
0.3
0.2
0.1
0
FEEDING RATE (g. per 30 min.)
-3 -2--1 0-1 2-3 4-5 6-7 8-9
2nd HATCHED CHICK AGE (days)

Figure 15

The relationship between feeding rate[1] and chick age[2] for A-chicks[3] of broods in which the B-chick survived at least 15 days post hatch, the B-chick died within 15 days of hatching, or the B-chick disappeared within 15 days of hatching, from 1979

1 Means are shown with standard errors. The number of 30 minute sampling periods and the number of broods observed can be attained from the corresponding figures (Figs 17, 18, 19).

2 B-chick age for each brood.

3 Means are based on feeding rates to chicks of broods with A and B-chicks alive, from 2 and 3-egg clutches.

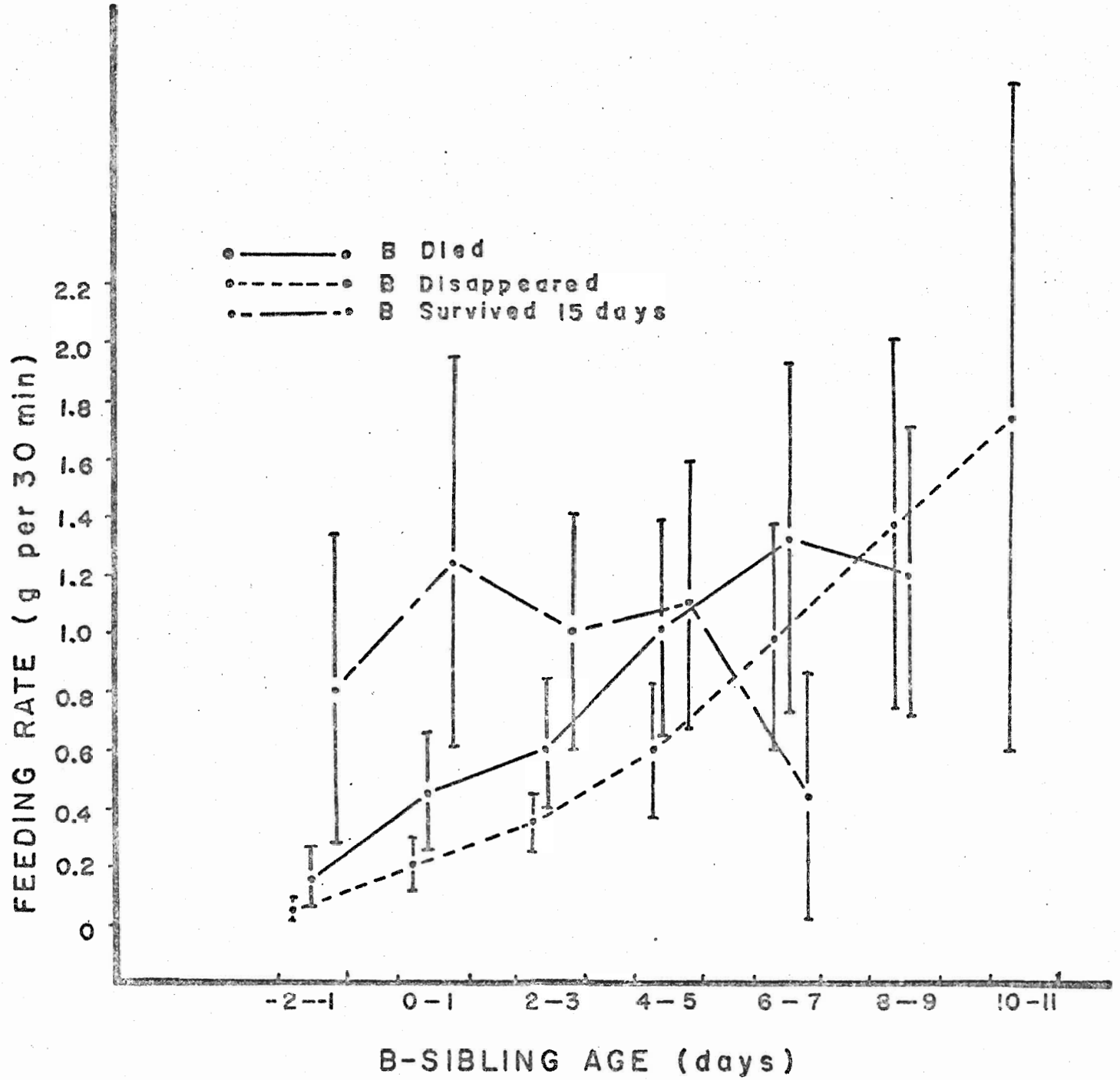

B Died
B Disappeared
B Survived 15 days
FEEDING RATE (g per 30 min)
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
-2--1
0-1
2-3
4-5
6-7
8-9
10-11
B-SIBLING AGE (days)

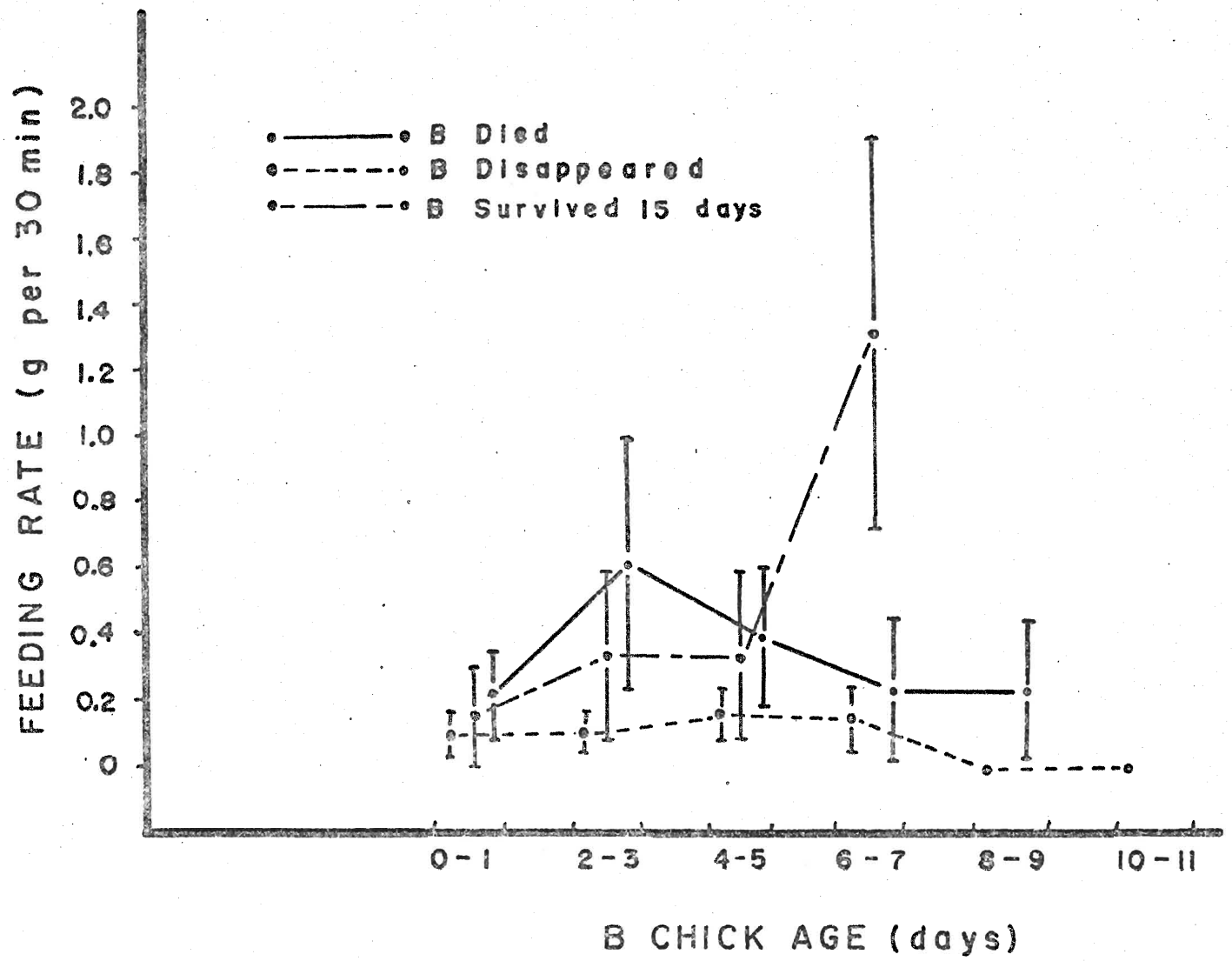
Figure 16

The relationship between feeding rate[1] and chick age[2] for B-chicks[3] of broods in which the B-chick survived at least 15 days post hatch, the B-chick died within 15 days of hatching, or the B-chick disappeared within 15 days of hatching, from 1979

1 Means are shown with standard errors. The number of 30 minute sampling periods and the number of broods observed can be attained from the corresponding figures (Figs 17, 18, 19).

2 B-chick age for each brood.

3 Means are based on feeding rates to chicks of broods with A and B-chicks alive, from 2 and 3-egg clutches.


B Died
B Disappeared
B Survived 15 days
FEEDING RATE (g per 30 min)
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
0-1
2-3
4-5
6-7
8-9
10-11
B CHICK AGE (days)

at ages 6-7 days (Fig 16).

Feeding rates to A and B-chicks from 1979 are shown together, according to specific brood categories (Figs 17, 18, 19). A-chicks of brood category 1 (survived) were fed, in general, at a faster rate than their B-siblings, except at ages 2-3 and 6-7 days, when feeding rates to A and B-chicks were similar (Fig 17). A-chicks were fed, in general, at a faster rate than B-chicks in brood category 2 (died), although feeding rates to A and B-chicks were similar at ages 0-3 days (Fig 18). Feeding rates to A and B-chicks of brood category 3 (disappeared) were similar at ages 0-1 days, however, from ages 2-11 days, A chicks were fed at faster rates (Fig 19).

Feeding Rates and Intra-Brood Food Apportionment

The percentage of total food fed to the least-fed chick (of A or B) in each brood was determined as a function of total feeding rate during ages 0-5, 6-10, and 11-15 days (B-chick age) in 1978 (Table 7). The result for age 0-5 and 6-10 days was a significant positive correlation between the % fed to the least-fed chicks and the total feeding rate to the brood during that period (Fig 20, Table 7). As feeding rates to the broods increased, apportionment within the brood became more equal. No significant correlation existed for the 11-15 day period in 1978. In 1979 a similar determination for B-chick age periods 0-5 days and 6-10 days found no significant correlations (Table 7). The mean % fed to least-fed chicks within broods was determined for age period 0-5, 6-10, and 11-15 days in 1978 and for age periods 0-5 and 6-10 days in 1979 (Table 8). Based on the mean % of food fed to the least-fed chicks, the intrabrood food apportionment was most even

Figure 17

The relationship between mean feeding rates[1] and chick age[2] for A and B-chicks[3] of broods in which the B-chick survived at least 15 days post hatch from 1979

1 Means are shown with standard errors and the number of 30 minute sampling periods, and the number of broods observed. Means included are based on at least two broods.

2 B-chick age for each brood

3 Means are based on feeding rates to chicks of broods with A and B-chicks alive, from 2 and 3-egg clutches.

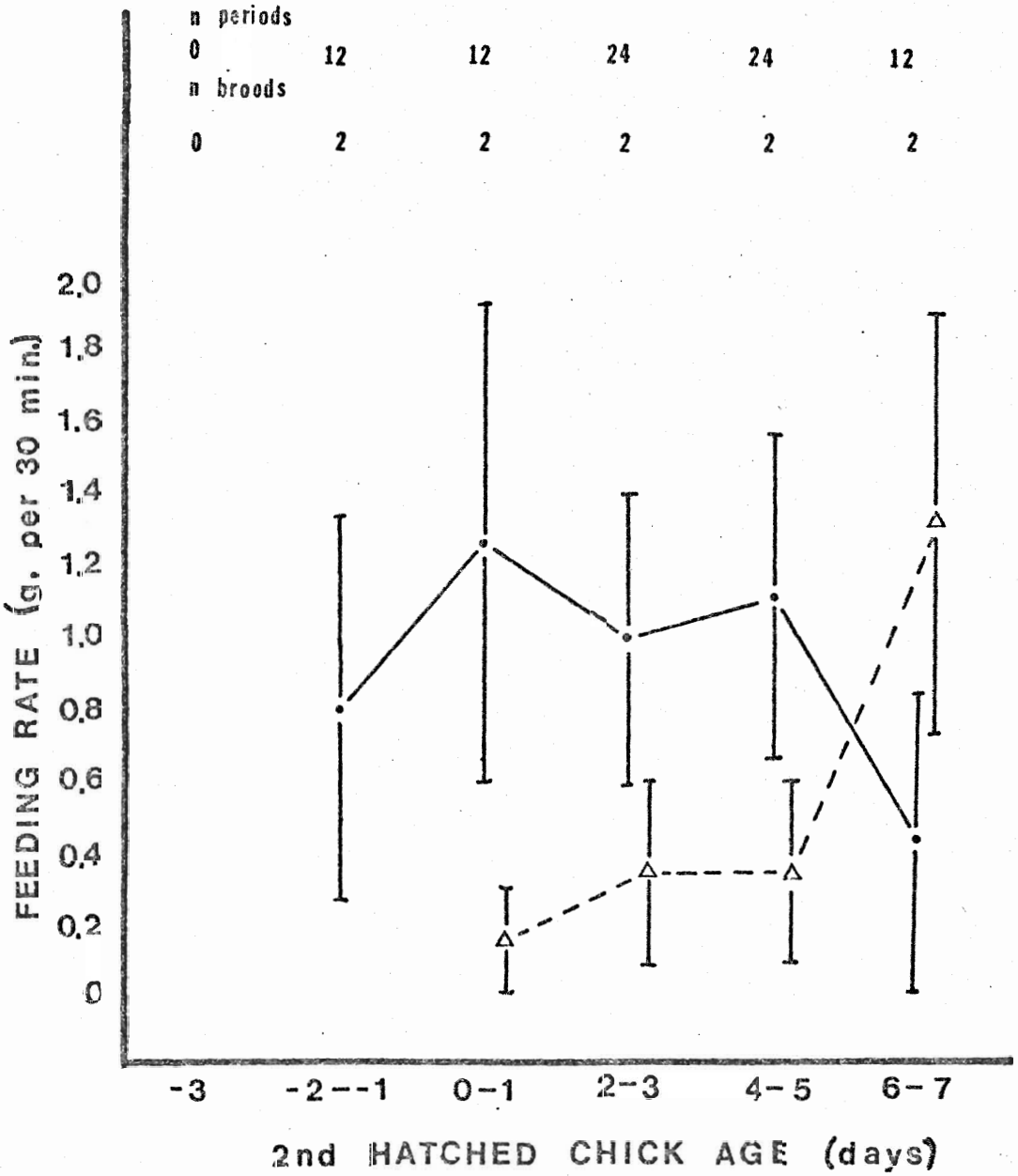

n periods
0
12
12
24
24
12
n broods
0
2
2
2
2
2
FEEDING RATE (g. per 30 min.)
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
-3
-2--1
0-1
2-3
4-5
6-7
2nd HATCHED CHICK AGE (days)

Figure 18

The relationship between mean feeding rates[1] and chick age[2] for A and B-chicks[3] of broods in which the B-chick died within 15 days of hatching, from 1979

[1] Means are shown with standard errors and the number of 30 minute sampling periods, and the number of broods observed. Means included are based on at least two broods.

[2] B-chick age for each brood.

[3] Means are based on feeding rates to chicks of broods with A and B-chicks alive, from 2 and 3-egg clutches.

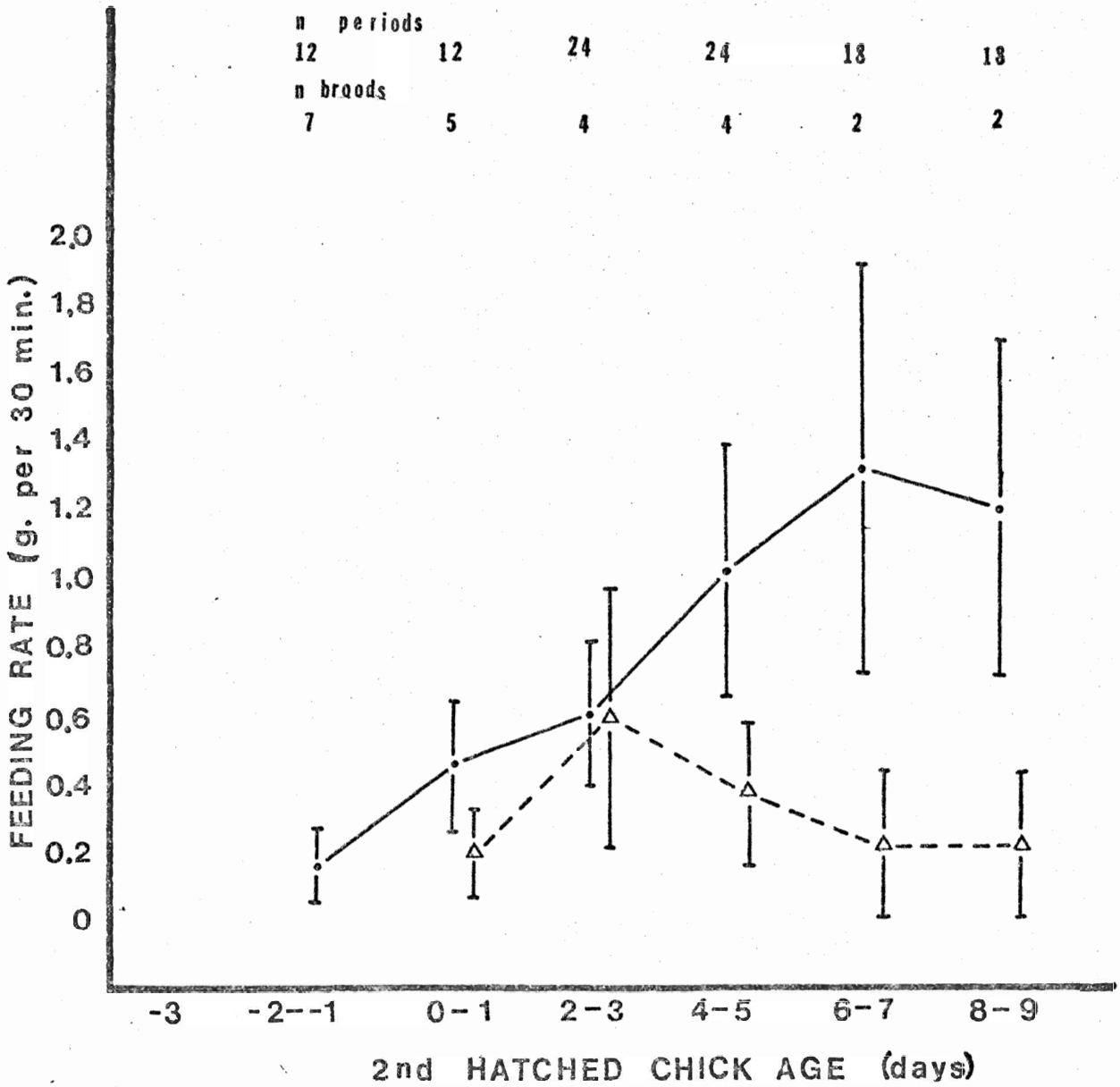

n periods
12 12 24 24 18 18
n broods
7 5 4 4 2 2
FEEDING RATE (g. per 30 min.)
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
-3 -2--1 0-1 2-3 4-5 6-7 8-9
2nd HATCHED CHICK AGE (days)

Figure 19

The relationship between mean feeding rates[1] and chick age[2] for A and B-chicks[3] of broods in which the B-chick disappeared within 15 days of hatching, from 1979

[1] Means are shown with standard errors and the number of 30 minute sampling periods, and the number of broods observed. Means included are based on at least two broods.

[2] B-chick age for each brood.

[3] Means are based on feeding rates to chicks of broods with A and B-chicks alive, from 2 and 3-egg clutches.

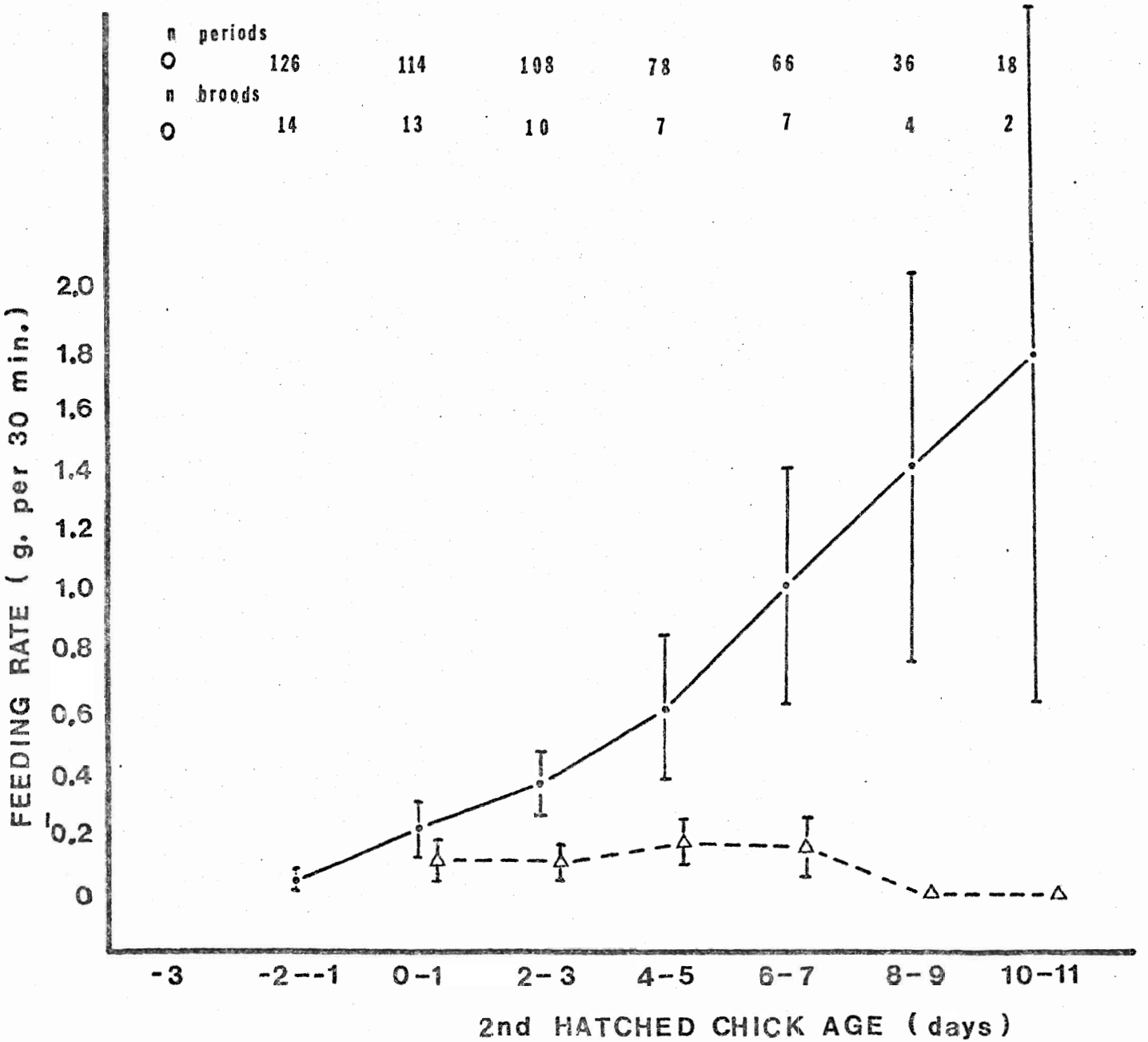

n periods
126 114 108 78 66 36 18
n broods
14 13 10 7 7 4 2
FEEDING RATE (g. per 30 min.)
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
-3 -2--1 0-1 2-3 4-5 6-7 8-9 10-11
2nd HATCHED CHICK AGE (days)

Table 7: Spearman Rank Correlation Coefficients[1] between Total Feeding Rates[2] and Percent Fed to the Least-fed Chick in the Brood

Year	Age[3] 0-5 Days	Age[3] 6-10 Days	Age[3] 11-15 Days
1978	rs = +0.6296 p < 0.01 N = 16	rs = +0.7412 P < 0.05 N = 7	rs = +0.205 P > 0.05 N = 5
1979	rs = +0.2122 P > 0.05 N = 10	rs = -0.0857 P > 0.05 N = 6	Sample Size Too small

[1]Only nests with complete feeding records (for the period tested), and at least two feedings recorded, were included.

[2]Total feeding rate was based on the period tested.

[3]B-chick ages.

Figure 20

The relationship between the percentage of food fed to the least-fed chick in the brood[1] and the total feeding rate to the brood[2] for the age period of zero to five days,[3] from 1978

[1] Least-fed chicks were fed the least during the age period considered.

[2] Total feeding rate was a mean rate for the age period considered. Only broods observed being fed at least twice were included.

[3] Age period is determined according to the B-chick age for each brood.

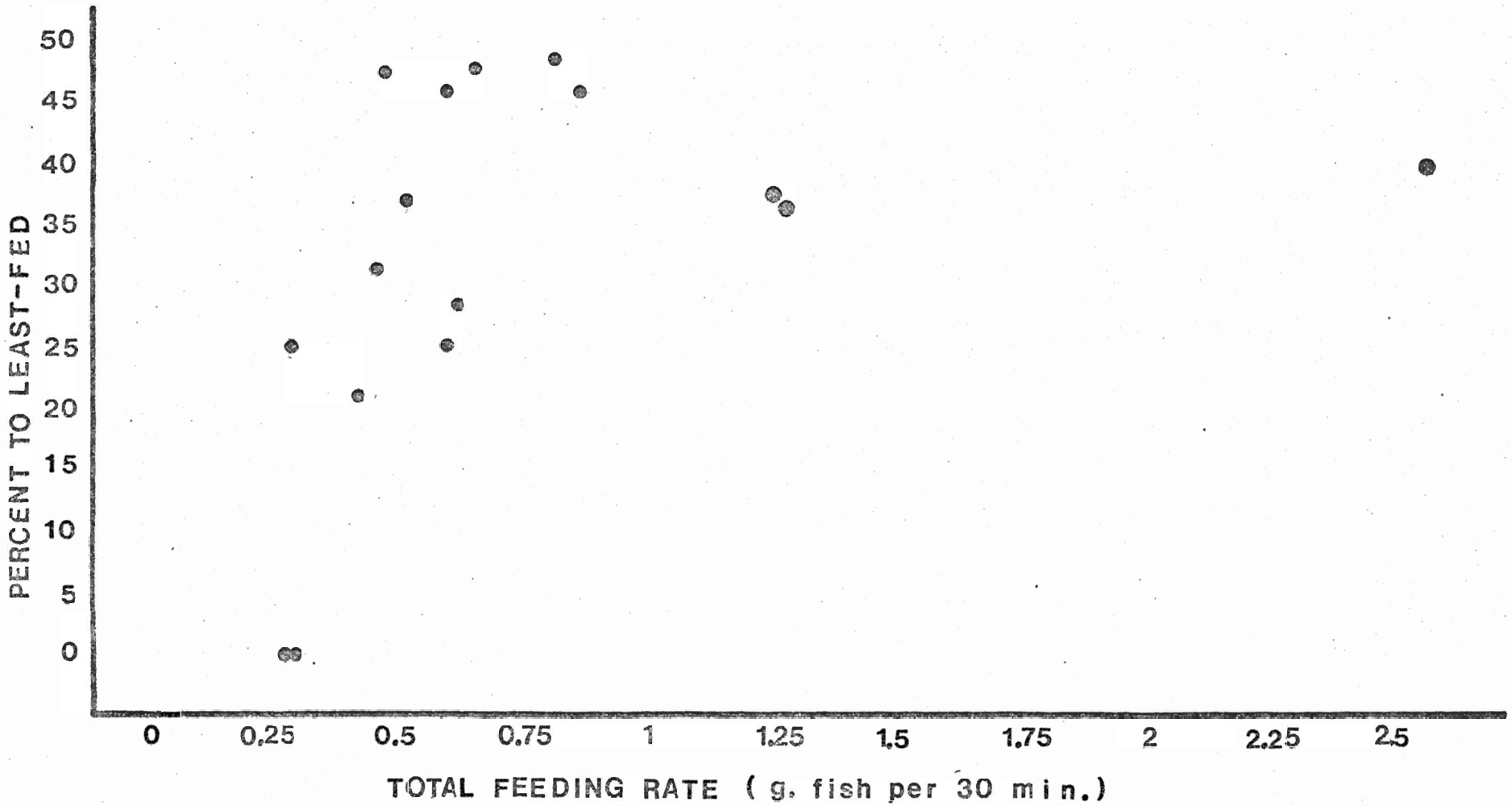

PERCENT TO LEAST-FED
50
45
40
35
30
25
20
15
10
5
0
0
0.25
0.5
0.75
1
1.25
1.5
1.75
2
2.25
2.5
TOTAL FEEDING RATE (g. fish per 30 min.)

Table 8: The Mean Percent of Total Food (brought to the brood during the period) Fed to Least-Fed Chicks, and the Hatching Order of Least-Fed Chicks in each Age Period Determined from 1978 and 1979

Year	Age Period[1] (days)	Mean % Fed to Least-Fed Chicks	Broods with A-Chick Least-Fed (n)	Broods with B-Chick Least-Fed (n)
1978	0-5	32.48	10	6
	6-10	11.91	2	5
	11-15	21.77	2	3
1979	0-5	29.43	2	8
	6-10	11.33	0	6

[1]Age period is based on B-chick age for each brood.

during the 0-5 day period in both years. During the 0-5 day (B-chick age) period in 1978, A-chicks were least-fed in 10 (62.5%) of the broods considered (Table 8). During the corresponding period in 1979, A-chicks were least-fed in only 2 (20%) of the broods considered. The difference between years was significant (Fisher Exact Test P = 0.0418). Excepting the 0-5 day (B-chick age) period in 1978, B-chicks were least-fed in more broods than were A-chicks (Table 8).

Hatch Order and Exposed Culmen Lengths

Comparisons of exposed culmen lengths were made for age classes where at least three paris of chicks were measured (Table 9). With the exception of age class 0-1 days, sample sizes were low. The culmen length of A-chicks were significantly greater than B-chicks at 0-1 and 20-21 days of age (Table 9). Although chicks were not measured in 1978, A-chicks appeared larger than their B-siblings.

FLEDGING AGES

A chick was considered fledged if it disappeared from the study area at age 30 days or greater. The mean fledge age (based on the age chicks were last recorded as present during a nest chick) for 1978 A-chicks in broods which fledged two chicks (n=16) was 34.5 $\pm$ 3.78 days. B-chicks in those broods (n=13) fledged, on average, at 37.5 $\pm$ 5.24 days. Sample sizes are different for A and B-chicks because 3 B-chicks left the colony before fledging (before fence erection) and were later found alive at age 30 or more days. The difference in fledging ages was nearly significant (Wilcoxon Rank Sum Test, W1 = 197.5, W2 = 237.5, n1 = 16, n2 = 13, P = 0.0655). A-chicks of 1978 broods which hatched at least A and B-eggs, fledged at 35.04 $\pm$ 3.768 days on average, while B-chicks fledged at 36.04

Table 9: Exposed Culmen Lengths of A versus B Siblings (1979)

Chick Age (days)	Pairs of Chicks Measured (n)	Mean Culmen Length, A-Chicks (±1 standard deviation) (cm)	Mean Culmen Length, B-Chicks (±1 standard deviation) (cm)	Paired T Statistic	Probability
0-1	46	1.65 ± (0.07)	1.62 ± (.07)	3.224	0.0024
2-3	5	1.83 ± (0.15)	1.69 ± (.03)	-2.055	0.1091
8-9	3	2.13 ± (0.30)	2.00 ± (.12)	-0.643	0.5863
20-21	5	3.54 ± (0.19)	2.85 ± (.30)	-4.923	0.0079

± 5.678 days on average. The difference was not significant (Wilcoxon Rank Sum Test, W1 = 569.5, W2 = 606.5, n1 = 22, n2 = 26, P = 0.535). A-chicks of 1979 broods which hatched at least A and B-eggs fledged at 37.48 ± 3.23 days on average while B-chicks fledged at 38.18 ± 3.52 days on average. The difference was not significant (Wilcoxon Rank Sum Test, W1 = 750.5, W2 = 269.5, n1 = 33, n2 = 11, P = 0.5601).

A-chicks in 1978 broods which hatched A and B-eggs fledged at age 34.5 ± 3.49 days on average while the corresponding A-chicks in 1979 fledged at 35.73 ± 3.25 days on average. The difference was significant (Wilcoxon Rank Sum Test, W1 = 312.5, W2 = 912.5, n1 = 19, n2 = 30, P = 0.0009).

Chick Fates

The fates of A and B-chicks from 2 and 3-egg clutches which hatched A and B-eggs are in Table 10. Chicks which survived until at least 30 days of age post-hatch were considered fledged. Unless otherwise noted, fledging success rates were calculated per egg hatched and nests included hatched both A and B-eggs. Chicks categorized as "probably fledged" or "unknown" (in 1978) were assumed to have fledged for fledging success rate comparisons between years. Making this assumption yields the same results in all comparisons of fledge success per egg hatched as treatments excluding "probably fledged" and "unknown" chicks. Furthermore, of all 1978 A-chicks, with known fates, that survived to age 12 days, 94% (n=47) fledged. Ninety-eight% (n=45) of 1978 A-chicks, of known fates, that survived to age 24 days, fledged. Eighty-four decimal one % (n=37) of 1978 B-chicks, of known fates, that survived to age 12 days fledged. All (n=37) 1978 B-chicks, of known fates, that survived to age 24 days fledged.

Table 10: Chick Fates of 1978 and 1979 2 and 3-egg Clutches that Hatched both A and B-eggs

	Year			
	1978		1979	
Chick Fate	Number of A-Chicks n (%)	Number of B-Chicks n (%)	Number of A-Chicks n (%)	Number of B-Chicks n (%)
Fledged	35(55.5)	28(44.4)	35(60.3)	13(22.4)
[1]Probably fledged	7(11.1)	0(0)	--	--
[2]Unknown	14(22.2)	4(4.8)	--	--
Died	2(3.2)	20(31.7)	9(15.5)	18(31.0)[3]
Disappeared	5(7.9)	11(17.5)	13(22.4)	26(44.8)[3]
Worker Error	0(0)	0(0)	1(1.7)	0(0)
Total	63(100)	63(100)	58(100)	58(100)[3]

[1]Disappeared between ages 24-29 days prior to permanent fence erection.

[2]Disappeared between ages 12-23 days prior to permanent fence erection.

[3]Nest 156 B-Chick was found nearly dead at age 13 and disappeared before the next check. It was omitted except in the total count and included in statistical analysis of fledging success.

There were no significant differences in fledging success rates of A and B-chicks from 2 or 3-egg clutches, and no C-chicks fledged in either year (Table 11). Accordingly, 2 and 3-egg clutches have been treated together and C-eggs and chicks have been excluded.

During 1978, A-chicks fledged at a significantly higher frequency than B-chicks ($X^2c = 20.34$, $P < 0.01$). The important chick fate category contributing to the fledge success differences was the significantly higher frequency of deaths by B-chicks compared with A-chicks ($X^2c = 15.915$, $P < 0.001$). Differences in disappearance rates between A and B-chicks were small ($X^2c = 1.79$, $P > 0.1$).

Fledging success rates per egg hatched, and,per pair, according to which eggs hatched,are shown for 1978 and 1979 in Table 12. During 1978, pairs hatching both A and B-eggs had the best total fledging per pair rate. A-chicks in clutches hatching only A-eggs did not fledge significantly more frequently than A-chicks in clutches hatching A and B-eggs ($X^2c = 0.540$, $P > 0.1$). B-chicks in clutches which hatched only B-eggs fledged significantly more frequently than B-chicks of clutches hatching A and B-eggs ($X^2c = 5.314$, $P < 0.05$).

During 1979, A-chicks fledged at a significantly higher frequency than B-chicks ($X^2c = 15.673$, $P < 0.001$). The greatest factor contributing to this result was the high frequency of B-chick disappearances compared to A-chicks ($X^2c = 5.91$, $P < 0.02$). B-chicks in 1979 died more frequently than A-chicks, however, the difference was not significant ($X^2c = 3.282$, $0.1 > P > 0.05$).

During 1979, pairs hatching both A and B-eggs had the best total fledging per pair rate (Table 12). A-chicks in clutches hatching only A-eggs did not fledge significantly more frequently than A-chicks in

Table 11: Chi Squared Comparisons of 2 versus 3-egg Clutch Fledging Success per Chick Hatched

Year	Comparison	X^2_c	Probability
	A-chicks	1.0290	P > 0.1
1978[1]	B-chicks	0.9559	P > 0.1
	A and B-chicks	2.1336	P > 0.1
	A-chicks	0.00004	P > 0.1
1979	B-chicks	0.0117	P > 0.1
	A and B-chicks	0.0630	P > 0.1

[1]Probable fledges and unknowns assumed fledged.

Table 12: A and B Fledge Success According to Egg Hatch of 2 and 3-egg Clutches

Year	Egg(s) Hatched	Number of A-Eggs Hatched	Number of A-Chicks Fledged	Number of A-Chicks Unknown and Probable Fledged	Number of B-Eggs Hatched	Number of B-Chicks Fledged	Number of B-Chicks Unknown and Probable Fledged	[1]A-Chick Fledging Rate (per hatch)	[1]B-chick Fledging Rate (per hatch)	[1]Total Fledging Rate (per pair)
	A only	13	12	1	--	--	--	1	--	1
1978	B only	--	--	--	12	9	2	--	0.9166	0.9166
	A and B	63	35	21	63	28	4	0.8889	0.5079	1.3968
	A only	7	3	--	--	--	--	0.4286	--	0.4286
1979	B only	--	--	--	8	5	--	--	0.625	0.625
	A and B	58	35	--	58	13	--	0.6034	0.224	0.8275

[1]Fledging rates include unknowns and probable fledges as fledged.

clutches hatching A and B-eggs ($X^2c = 0.231$, $P > 0.1$). However, B-chicks in clutches hatching only B-eggs fledged significantly more frequently than B-chicks in clutches hatching A and B-eggs ($X^2c = 3.854$, $P < 0.05$).

Fledging success of 2 and 3-egg clutches was significantly higher in 1978 than 1979 ($X^2c = 18.737$, $P < 0.001$). A-chicks fledged significantly more frequently in 1978 than 1979 ($X^2c = 11.709$, $P < 0.001$). B-chicks also fledged significantly more frequently in 1978 than 1979 ($X^2c = 9.233$, $P < 0.01$). In 1978, 17 pairs fledged both A and B-chicks, significantly more than the four pairs in 1979 which fledged A and B-chicks ($X^2c = 7.153$, $P < 0.01$).

In 1979, A-chicks disappeared ($X^2c = 3.92$, $P < 0.05$) and died ($X^2c = 4.173$, $P < 0.05$) significantly more frequently than 1978 A-chicks. B-chicks disappeared significantly more frequently in 1979 than 1978 ($X^2c = 9.84$, $P < 0.01$) but died at a similar frequency ($X^2c = 0.0313$, $P > 0.1$).

Causes of Mortalities

Crude autopsies were performed on 61 chicks of known ages found dead during 1978 and 1979 (Appendix Table II). Chicks with external damage (aside from slight culmen damage caused by abrasion on the fence) represented 22.95% (n=14) of the total sample (n=61). Most dead chicks handled were emaciated, and 80%(n=46)had empty stomachs. Chicks which lacked external damage and had empty stomachs made up 72%(n=41) those examined. Independent autopsies of two chicks by a veterinarian revealed starvation as the likely cause of death.

Causes of Disappearances

Since the colony was checked carefully every two to four days, and fencing was effective, the disappearance of a chick meant actual removal of the chicks, alive or dead. On five occasions, Ring-billed Gulls were

observed causing agitation in the tern colony (Caspian Terns called, dove at, and pursued the intruder) and flying off carrying a tern chick of between 0-7 days of age. Herring Gull predation on older tern chicks (7-21 days of age) was observed three times in the study colony and five times in the adjacent Caspian Tern colony. One Ring-billed Gull was observed picking up and carrying off a dead Caspian Tern chick. However, in the 12 cases where the condition of chicks when found dead was noted, 5 were fresh while 7 were at some stage of decay, suggesting indirectly that scavenging was not common. One final possible source of disappearance, not directly observed, was nocturnal predation and/or scavenging.

In the one observed case of scavenging, the Ring-Billed Gull involved pecked at, then picked up, the chick and flew off without haste, or harassment by Terns. Lone Ring-billed Gulls were observed periodically wandering through the tern colony, pecking at regurgitated pellets and abandoned fish. These birds were rarely attacked (or harassed) unless they walked within 0.5 meters of a tern nest with an adult present. Dead chicks were often found more than 0.5 meters from the nearest tern nest.

An attempt was made to identify specific agents of chick disappearance through analyses of time-lapse films (Appendix Table III). The analysis provided some evidence suggesting that nocturnal losses occurred in seven (46.66%) cases (case numbers 2, 3, 6, 7, 10, 12, and 15; Appendix Table III). Predation was suggested in five (33.33%) cases, two by Ring-billed Gulls (case numbers 5, and 14), one by Herring Gulls (case number 9) and two by unseen agents (case numbers 4 and 11; Appendix Table III). One case suggested either predation or scavenging by a Ring-billed Gull (case number 1) and one case provided no useful information

(case number 13; Appendix Table III).

Mortality, Disappearances and Chick Age

Ages when chicks were last recorded alive and present during a nest check were plotted for chicks that died or disappeared from broods which hatched A and B-eggs in 1978 (Fig 21) and 1979 (Fig 22). In 1978, only two A-chicks were found dead while B-chicks died over a wide range of ages (0-19 days; Fig 21). Five A-chicks disappeared between ages 0-24 days, however, none of those disappeared between 4-14 days of age (Fig 21). B-chicks disappeared from ages 0-13 days, with a peak in the number of disappearances at 4-5 days of age (Fig 21).

Ages of disappearance were compared with ages of death for all 1978 A-chicks. The mean disappearance age (11.6 $\pm$ 9.91 days) did not differ significantly from the mean age of mortality (6 $\pm$ 4.24 days; Wilcoxon Rank Sum Test, W1 = 21.5, W2 = 6.5, n1 = 5, n2 = 2, P = 0.6985). The same comparison was made for B-chicks, from clutches which hatched A and B-chicks, that died or disappeared in 1978. The mean disappearance age (6.1 $\pm$ 3.99 days) did not differ significantly from the mean age of mortality (8.1 $\pm$ 5.51; Wilcoxon Rank Sum Test, W1 = 180, W2 = 348, n1 = 12, n2 = 20, P = 0.4958).

During 1979, A-chicks died from ages 4-28 days while B-chicks died from ages 0-22 days (Fig 22). A-chicks disappeared from ages 0-10 days although most (n = 9, 69.2%) disappeared from ages 0-3 days (Fig 22). B-chicks disappeared from ages 0-14 days and disappearances were common until age 10 days.

Ages of disappearance and mortality were compared for all 1979 A-chicks. The mean age of disappearance (2.75 $\pm$ 3.17 days) was significantly earlier than the mean age of mortality (12.9 $\pm$ 9.16 days;

Figure 21

The relationship between the frequency[1] of mortality[2] and disappearance[3], and chick age[4] of A and B-chicks[5] in 1978[6]

[1] Fates of 15 A-chicks and B-chicks which disappeared from the study area prior to July 4 (fence erection) at ages 12 to 22 days were unknown. Seven A-chicks which disappeared prior to July 4 at ages 23 to 29 days were considered to have probably fledged.

[2] Those found dead during nest checks were considered mortalities.

[3] Those not found during nest checks were considered to have disappeared.

[4] The age of disappearance or mortality was that age when a chick was last recorded alive during a nest check.

[5] A and B-chicks of nests which hatched both A and B-eggs, from 2 and 3-egg clutches, were considered.

[6] Based on 63 nests.

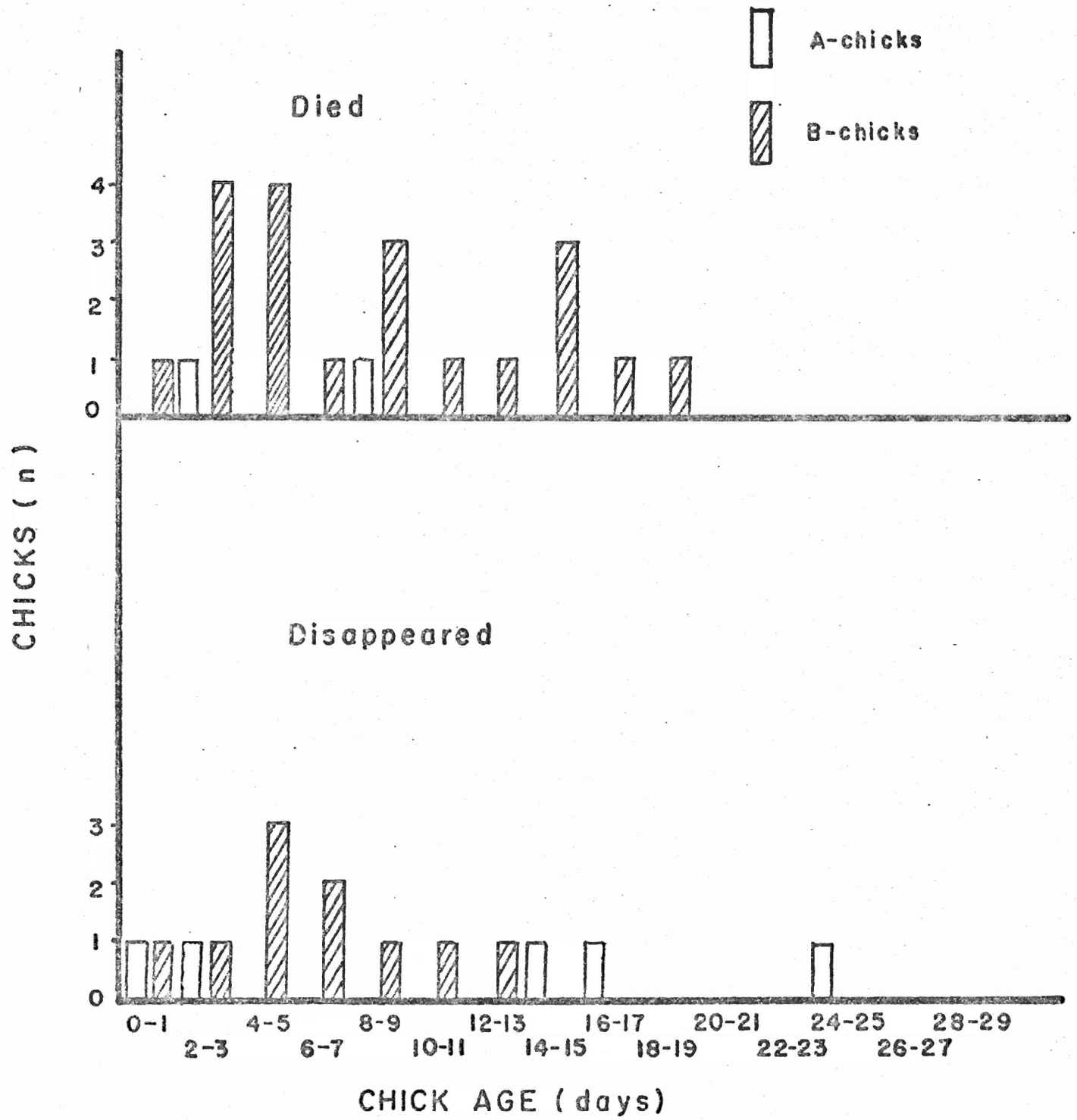

A-chicks
B-chicks
Died
Disappeared
CHICKS (n)
0
1
2
3
4
0
1
2
3
0-1
2-3
4-5
6-7
8-9
10-11
12-13
14-15
16-17
18-19
20-21
22-23
24-25
26-27
28-29
CHICK AGE (days)

Figure 22

The relationship between the frequency of mortality[1] and disappearance[2], and chick age[3] of A and B chicks[4] in 1979[5]

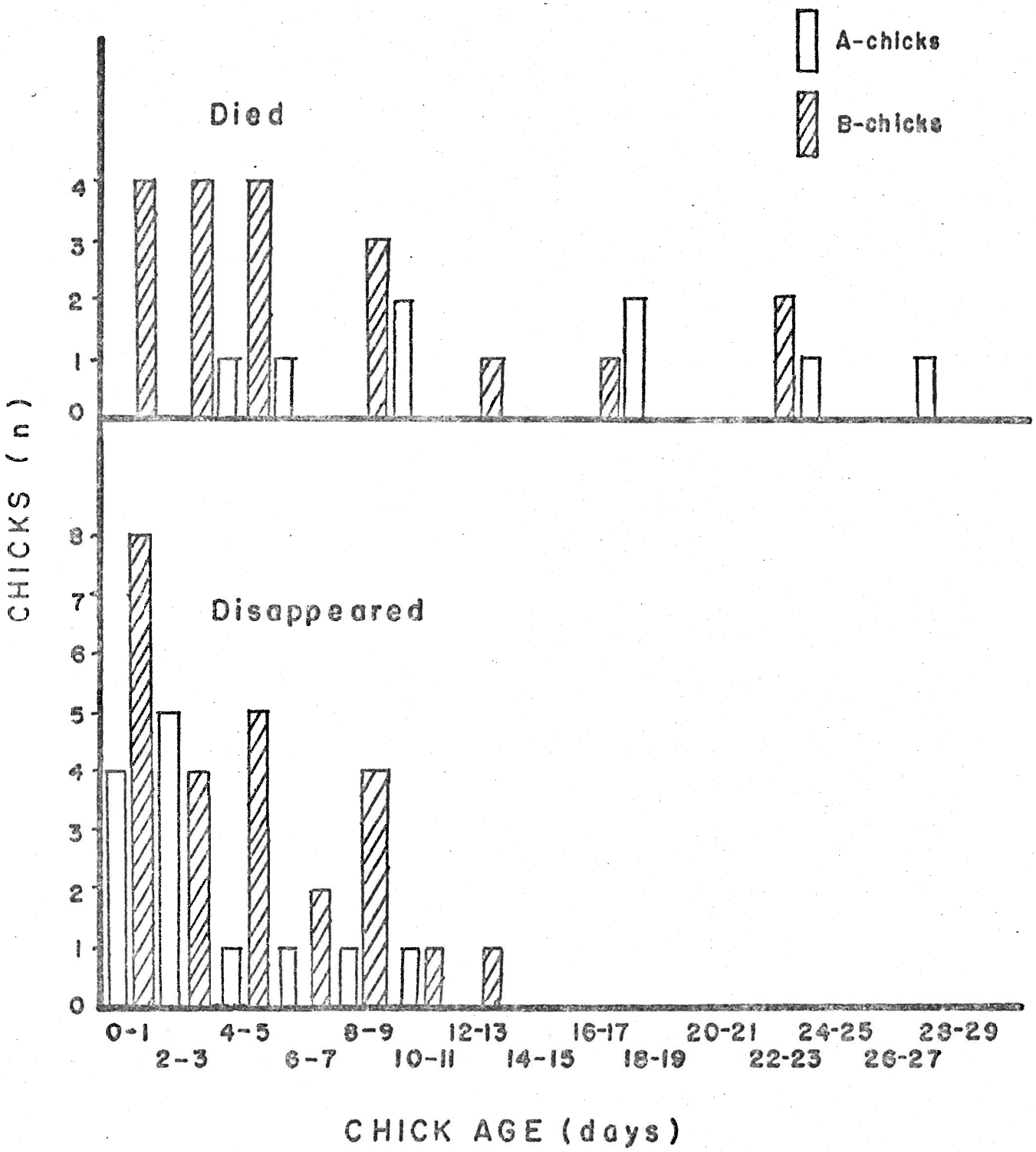
[1] Those found dead during nest checks were considered mortalities.

[2] Those not found during nest checks were considered to have disappeared.

[3] The age of mortality or disappearance was that age when a chick was last recorded as alive during a nest check.

[4] A and B-chicks of nests which hatched both A and B-eggs, from 2 and 3-egg clutches, were considered.

[5] Based on 54 nests.


A-chicks
B-chicks
Died
Disappeared
CHICKS (n)
0
1
2
3
4
5
6
7
8
0-1
2-3
4-5
6-7
8-9
10-11
12-13
14-15
16-17
18-19
20-21
22-23
24-25
26-27
28-29
CHICK AGE (days)

Wilcoxon Rank Sum Test, W1 = 158, W2 = 193, n1 = 16, n2 = 10, P = 0.0024). B-chicks from 1979 broods which hatched A and B-eggs died at age 6.79 ± 7.11 days on average and disappeared at age 4.16 ± 3.70 days. The difference was not significant (Wilcoxon Rank Sum Test, W1 = 469, W2 = 521, n1 = 19, n2 = 25, P = 0.3313). A comparison of 1979 A and B-chicks revealed no significant difference in ages of disappearance (Wilcoxon Rank Sum Test, W1 = 513, W2 = 228, N1 = 25, n2 = 13, P = 0.4418).

B-chick Survival After A-sibling Loss

During 1978, seven A-chicks from clutches hatching both A and B-eggs died or disappeared (two died, five disappeared). Four B-siblings of those A-chicks survived to at least fledging age. In 1979, 21 A-chicks from clutches hatching both A and B-eggs died or disappeared (eight died, 13 disappeared). Eleven (52.4%) B-siblings of those A-chicks survived to at least fledging age.

Egg-weights and Chick Fates

A-eggs which produced chicks that fledged had significantly greater fresh weights than those which produced A-chicks that did not fledge (Table 13). Fresh egg-weights of A-chicks which produced chicks that died before age 30 days were not significantly different from fresh egg-weights of those producing chicks which fledged (Table 13). Fresh egg-weights of A-eggs producing chicks that fledged were significantly greater than those producing chicks that disappeared (Table 13).

Fresh weights of B-eggs that produced chicks which fledged were not significantly different from those which produced chicks that died or disappeared before age 30 days (Table 13).

The relationship between fresh egg weights and chick disappearance

Table 13: Wilcoxon Rank Sum Test Comparisons of Fresh Egg-weights According to the Fates of Chicks Hatching from those Eggs, in 1979

Lay Order	Chick Fate	Mean Fresh Egg Weight (g)	Standard Deviation	W1	W2	n1	n2	P
A	Fledged	71.6	4.81	632.5	357.5	24	20	0.0301
	Not Fledged	67.9	5.83					
A	Fledged	71.6	4.81	371.5	93.5	24	6	1.00
	Died	71.7	3.40					
A	Fledged	71.6	4.81	543.0	160.0	24	13	0.0059
	Disappeared	66.1	6.18					
B	Fledged	68.0	5.07	240.5	662.5	10	32	0.4603
	Not fledged	66.6	4.52					
B	Fledged	68.0	5.07	112	78	10	9	0.3477
	Died	65.9	4.57					
B	Fledged	68.0	5.07	348	180	22	10	0.555
	Disappeared	66.7	4.63					

is in Figure 23. The distribution of A-chick disappearances did not follow the frequency curve of A-egg fresh weights, especially in the upper range of egg weights (above 70 grams; Fig 23). Of 19 A-eggs weighing 71 grams or more, two (10.5%) produced chicks that disappeared. Of 20 A-eggs weighing less than 71 grams, nine (45%) produced chicks which disappeared. The distribution of B-chick disappearances followed the frequency curve of B-eggs fresh-weights (Fig 23).

In order to indirectly test the possibility that parents producing large A-eggs were better parents, A-egg weights were compared according to B-chick fates. A-egg weights of broods fledging B-chicks were similar to A-egg weights of broods in which B-chicks died (Wilcoxon Rank Sum Test, W1 = 148, W2 = 105, n1 = 12, n2 = 10, P = 0.5310) or disappeared (Wilcoxon Rank Sum Test, W1 = 347.0, W2 = 214.0, n1 = 21, n2 = 12, P = 0.7222).

A correlation of fresh egg weights and initial exposed culmen measurements revealed no significant correlations for A (Spearman Rank Correlation, rs = +0.234, $P > 0.05$) or B-eggs and chicks (Spearman Rank Correlation, rs = +0.107, $P > 0.05$).

Intra-brood Hatching Synchrony and Fledging Success

The mean hatching synchrony is the interval in days between hatching of A and B-eggs and is shown as a function of fledging success in Table 14. Sample sizes were low and standard errors large, however, in 1978, broods that fledged A-chicks or A and B-chicks were generally less synchronous than those which fledged B-chicks or none at all. In 1979, broods fledging A-chicks or A and B-chicks were, on average, less synchronous than those fledging only B-chicks. Those fledging none were, on average, relatively asynchronous (Table 14).

Figure 23

The relationship between frequency of fresh-egg weights[1] and disappearances of chicks hatched from those eggs[2] from 1979

[1] Eggs were weighed during nest checks, within 48 hours of egg lay. Weights were rounded to the nearest gram (rounded down in the case of 0.5 grams). Eggs which did not hatch were excluded.

[2] Disappearances are indicated by x or 0 which appear above the egg weight category for the individual which disappeared.

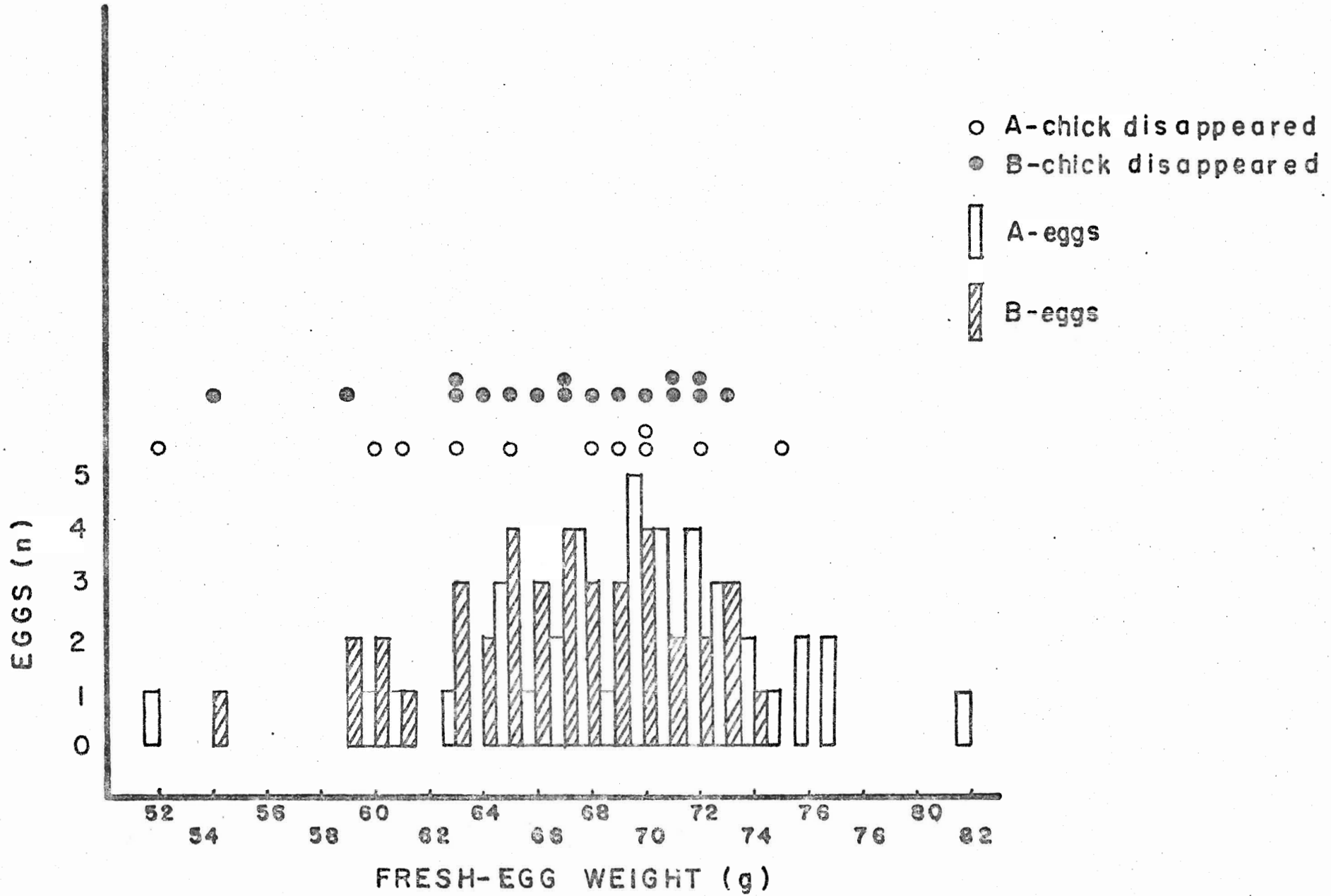

A-chick disappeared
B-chick disappeared
A-eggs
B-eggs
EGGS (n)
0
1
2
3
4
5
52
54
56
58
60
62
64
66
68
70
72
74
76
78
80
82
FRESH-EGG WEIGHT (g)

Table 14: Mean Hatching Interval between A and B-eggs[1] According to Fledging Success of A and B-chicks

Year	Chicks Fledged	Mean Interval between Hatching of A and B-Eggs (days)	Standard Error	Sample Size (2-egg clutches)
1978	None	0.5	0.5	2
	B only	1	0.577	3
	A only	1.5	0.167	10
	A and B	1.75	0.559	8
1979	None	2	0.298	10
	B only	1.29	0.607	7
	A only	1.81	0.131	27
	A and B	2	0	1

[1]From 2-egg clutches.

Clutch Size and Hatching and Fledging Success

Hatching and fledging success according to clutch size is in Table 15. In 1978, 2-egg clutches hatched significantly better than 1-egg clutches ($X^2c = 22.76$, $P < 0.001$; Tables 15, 16). Two-egg clutches from 1979 hatched significantly better than 1-egg clutches ($X^2c = 15.76$, $P < 0.001$; Tables 15, 16). Excepting one egg that failed to hatch, egg losses to 1979 1-egg clutches occurred within 2 days of the first nest check of those eggs (eggs disappeared, or were destroyed, or deserted). Two-egg clutches hatched A and B-eggs at a success rate similar to 3-egg clutches (1978, $X^2c = 0.0674$, $P > 0.1$; 1979, $X^2c = 0.055$, $P > 0.1$; Tables 15, 16).

One-egg clutches in 1978 fledged more chicks on a per hatch basis than did 2-egg clutches (Table 15), however, the difference was not significant ($X^2c = 1.533$, $P > 0.1$; Table 16). On a per pair basis, 2-egg clutches did significantly better at fledging than 1-egg clutches ($X^2c = 7.691$, $P < 0.01$, however, as was the case in 1979, it is likely that many eggs from 1-egg clutches were destroyed or deserted.. One-egg clutches in 1979 fledged more chicks on a per chick-hatched basis than 2-egg clutches (Table 15), however, the difference was not significant ($X^2c = 1.225$, $P > 0.1$). Excluding eggs that were lost or deserted within two days of first census, 1979 1-egg clutches fledged 0.625 chicks per nest, a rate similar to that of 1979 2-egg clutches ($X^2c = 1.827$, $P > 0.1$; Table 16).

Excluding C-eggs and chicks from consideration, 1978 3-egg clutches fledged more chicks per pair than 2-egg clutches (Table 15). However, the difference was not significant ($X^2c = 1.18$, $P > 0.1$; Table 16). In 1979 3-egg clutches fledged more chicks per pair than 2-egg clutches

Table 15: Hatching and Fledging Success Rates According to Clutch Size, from 1978 and 1979

Clutch Size	Clutches (n)	Hatched (n)	Hatch[1] per Egg	Fledge per Egg[2]	Fledge per Chick[2]	Fledge per Nest
1	38	7	0.184	0.184	1	0.1842
2	94	117	0.622	0.441	0.709	0.883
3	27	34	0.630	0.537	0.853	1.074
1	21	7	0.333	0.238	0.714	0.238
2	78	120	0.769	0.329	0.425	0.654
3	7	15	0.714	0.357	0.454	0.714

[1]C-eggs and chicks were excluded (in 1978 12 of 27 C-eggs hatched, none of those chicks fledged; in 1979 four of seven C-eggs hatched, none of those chicks fledged).

[2]Assuming "unknown" and "probably fledged" did fledge.

Table 16: The Numbers of A, B, and C-eggs and Chicks Laid, Hatched, and Fledged from 1, 2, and 3-egg Clutches in 1978 and 1979

Year	Clutch Size	A-Eggs (n)	Hatched A-Eggs (n)	A Fledged (n)	B-Eggs (n)	B Hatched (n)	B Fledged (n)	C-Eggs (n)	C Hatched (n)	C Fledged (n)
1978	1	38	7	7	--	--	--	--	--	--
1978	2	94	59	52[1]	94	58	31[2]	--	--	--
1978	3	27	17	17[3]	27	17	12	27	12	0
1979	1	21	7	5	--	--	--	--	--	--
1979	2	78	59	34	77[4]	61	17	--	--	--
1979	3	7	6	4	7	5	1	7	4	0

[1]Maximum number of fledged chicks (includes 13 "unknown" and five "probably fledged" chicks, see text).

[2]Maximum number of fledged chicks (includes six "unknown" chicks, see text).

[3]Maximum number of fledged chicks (includes two "unknown" and two "probably fledged" chicks, see text).

[4]One B-egg with an unknown fate was excluded.

(Table 15), however, the difference was not significant ($X^2c = 0.004$, $P > 0.1$; Table 16).

Clutch Size and Egg Weights

Fresh egg weights of 1-egg clutches (66.75 ± 6.85 gms on average) were lighter in weight than A-eggs of 2-egg clutches (70.30 gms ± 5.82 gms on average). The difference was nearly significant (Wilcoxon Rank Sum Test, W1 = 1926.5, W2 = 351.5, n1 = 53, n2 = 14, P = 0.0558). Fresh weights of A-eggs in 3-egg clutches (70.30 ± 7.00 gms) were similar to those of A-eggs in 2-egg clutches (70.30 ± 5.82; Wilcoxon Rank Sum Test, W1 = 1552, W2 = 159, n1 = 53, n2 = 5, P = 0.7606). The fresh weights of B-eggs in 3-egg clutches (70.20 ± 5.25 gms) were similar to those of B-eggs in 2-egg clutches (65.90 ± 7.75; Wilcoxon Rank Sum Test, W1 = 1383.5, W2 = 156.5, n1 = 51, n2 = 4, P = 0.1539).

Fresh weights of A-eggs in 3-egg clutches (72.00 ± 6.78 gms) were similar to those of B-eggs in 3-egg clutches (70.20 ± 5.25 gms; Paired T Test, T = 1.40, n = 4, P = 0.256). The fresh weights of C-eggs (67.00 ± 2.00gms) were similar to those of A-eggs in 3-egg clutches (72.00 ± 6.78 gms; Paired T Test, T = 2.07, n = 4, P = 0.1302), however, the sample size of 3-egg clutches was very small (n=4). Although no measurements were made in 1978, C-eggs were always noticeably smaller than A or B-eggs in the same clutch.

DISCUSSION

Observer Effects

The data collection process resulted in a degree of unavoidable disturbance to the colony I studied. The reduced hatching success of 1978 compared with 1979 (Table 3) was the result of disturbances. When researchers were in the colony in 1978, adult terns left their eggs unprotected from predation by Ring-billed Gulls. By contrast, in 1979, the use of nest domes (see Methods) prevented most disturbance-induced egg losses. However, in-colony researcher activities caused some desertion of newly initiated clutches in both years. Hence, the recorded hatching success of 1-egg clutches was probably artificially low.

Disturbance-induced egg-loss has been reported in a colony of Glaucous-winged Gulls (Gillet et al. 1975). Similarly in Herring Gulls, Hunt (1972) related lower hatching success to the frequency of picnicker visits. Nest desertions following disturbances of Caspian Tern colonies have been reported anecdotally (O'Donoghue and Gowanlock 1979, Bergman 1953, Vaisanen 1973, and Penland 1976).

Nisbet and Drury (1972) reported occurrences of Common and Roseate Tern chick mortality caused by chicken wire fencing. In my study area, although no deaths were attributed to fencing, some chicks received abrasions on the upper bill from collisions with the chickenwire fencing. During researcher visits, older chicks ($\geq$ 8 days) typically ran for cover and occasionally regurgitated whole fish. Following nest chicks, observations from the blind revealed that parents began to land on the colony within 30 sec of researcher departure. Chicks returning then, to their nests, were sometimes pecked by adult neighbors, however only one serious attack was observed. Parents prevented from feeding their chicks during

nest checks did so immediately after researcher departure from the colony. Although the effects of the 1979 disturbances were not directly tested, I assume that these were small relative to the 1978 egg losses.

The Eggs

Clutch Initiation

Clutches were initiated earlier in 1978 than 1979 (Figs. 2, 3), but the causal factors behind this are unknown. Laying cannot begin until sufficient food is available to allow egg production with minimal risk to the females' survival (Perrins 1970). Food availability appears to control egg laying dates in European Swifts (O'Connor 1979), Common Terns (Nisbet et al. 1978), and Audubon's Shearwater (Puffinus Iherminieri, Harris 1969). Positive correlations between temperature and laying in Arctic Terns (Evans and McNicholl 1972, Lemmetyinen 1973a) may have been due to food availability varying with temperature. Suggestively, mean daily temperatures were higher during the 1978 clutch initiation period compared with 1979. However, temperature is not the only factor affecting food availability. For example, higher winds can render food less available by driving the fish deeper into the water (to avoid surface turbulence; see Dunn 1975, Veen 1977). Unlike the temperature, windspeed was more favorable (lower) in 1979 than 1978 (Table 1).

Clutch Sizes

Fewer clutches of 3-eggs were laid in 1979 than 1978 in this study (Table 2). This may have been a result of food availability differences during egg laying. Shugart et al. (1978) attributed differences in mean clutch sizes in Caspian Tern colonies within the Great Lakes to differential food availability around colony sites. Lemmetyinen (1973b)

reported more frequent occurrences of 3-egg clutches on inner archepelago islands in Finland which he assumed were richer in food than the outer islands. Clutch sizes may have been reduced because of weather related food shortages in Arctic Terns (Hawksley 1957, Evans and McNicholl 1972), European Swifts (O'Connor 1979), and House Martins (Bryant 1975).

Clutch Size, Egg Weights and Season

The frequency of 3-egg clutches declined with the clutch initiation date (Figs. 2, 3). Seasonal declines of clutch sizes were reported in Caspian Terns (Soikkeli 1973a), Ring-billed Gulls (Ryder 1975), Red-billed Gulls (Mills, 1979), Black-legged Kittiwakes (Coulson and White 1961), and Herring Gulls (Davis 1973, Parsons 1975b). I found that fresh egg-weights declined with laying data (significantly for B-eggs). Factors affecting egg production (e.g., food availability) influence both clutch size and egg weights (Mills 1979). Egg size or weight declines, as a function of laying data, were reported in Red-billed Gulls (Mills 1979), Herring Gulls (Parsons 1972, Davis 1973) and Black-legged Kittiwakes (Coulson and Thomas 1978). The decline in Herring Gull fresh egg-weights occurred despite assumed improvements in food availability (Parsons 1975a). Declines in egg size or fresh egg-weight and/or clutch sizes according to laying date, were partly a function of parental age (Davis 1973, Parsons 1976, Coulson and Thomas 1978), however parental age did not account fully for the effect in Herring Gulls (Parsons 1976) and Red-billed Gulls (Mills 1979). Mills (1979) concluded that foraging ability and food availability were the primary factors controlling egg weights and clutch sizes in Red-billed Gulls.

Egg Weights and Laying Order

Caspian Tern eggs in my study represented a large investment, measured in terms of adult weight (A-eggs averaged 9.6% and B-eggs averaged 9%). Differences in egg weights within a clutch display the earliest differential apportionment of parental investment. B-eggs were significantly lighter than A-eggs (6.1% difference). A-egg weights correlated positively with B-egg weights. A-egg weights were also positively correlated with the egg-weight differences between A and B-eggs (within the same clutch). Thus parental investment increases favored A-eggs over B-eggs. The biological relevance of increased A-egg weight is discussed in a later section (Egg Weights and Chick Fates).

Egg weight or size differences between A and B-eggs of Herring Gulls (Parsons 1976) and Red-billed Gulls (Mills 1979) were small (2 and 2.2% respectively) and non-significant. Red-billed Gulls, like Caspian Terns, most commonly lay 2-egg clutches (Mills 1979). Egg weight differences in my study more closely approached differences between A and C-egg weights in other larids (e.g., 11% in Herring Gulls, Parsons 1976; 9.4% in Lesser Black-backed Gulls, Paludan 1951 cited in Parsons 1976; 7% in Laughing Gulls, Preston and Preston 1953 cited in Parsons 1976; and 7.3% in Black-legged Kittiwakes, Coulson 1963 cited in Parsons 1976).

Laying and Hatching Intervals and Hatching Synchrony

In my study A-eggs were incubated longer than B-eggs, probably because of ineffective early incubation, and slightly larger size of A eggs. Larger eggs have been shown to require longer incubation in House Martins (Bryant 1972) and Herring Gulls (Parsons 1972). Longer incubation of A-eggs in my study reduced the hatching interval from that of

the laying interval. While the laying interval was greater in 1978 than 1979, the hatching interval was similar both years. Increased laying intervals may be a response to, or a result of, decreased food availability (Bryant 1978a, O'Connor 1979). Increased laying intervals reduce the daily cost of egg production (Ricklefs 1974). The earlier clutch initiations and greater frequency of 3-egg clutches in 1978 compared with 1979 appears inconsistent with greater laying intervals in 1978 than 1979. Thus no conclusions can be drawn regarding the relative food availability during egg laying of the two years.

Hatching Success

The use of nest domes in 1979 reduced the loss of eggs to Ring-billed Gull predation during periods of investigator activity in the colony. For this reason 1979 data are considered to be more representative of hatching success at the South Limestone Islands Caspian Tern colony. As mentioned above, the low hatching success of 1-egg clutches (Table 15) may have been an artifact of human induced nest-desertion, even in 1979. Excepting 1-egg clutches, hatching success did not vary according to egg size (in 1979) or clutch size (Table 15). The hatching success of 2 and 3-egg clutches in 1979 (78.5%) was similar to that reported (81%) for other Great Lakes Caspian Tern colonies (Ludwig 1965).

Various Gull species have been identified as egg predators of Sandwich Terns (Sterna sandvicensis, Fuchs 1977), Royal terns (Sterna maxima, Buckley and Buckley 1972), Herring Gulls (Parsons 1975a) and Lesser Black-backed Gulls (Davis and Dunn 1976). Soikkeli (1973a:199) reported Caspian Tern egg losses caused "by predation by other Caspian Terns and perhaps gulls nesting close to the colony." However, Soikkeli did not observe undisturbed birds and did not present data addressing

this point. Allen (1977) analyzed Caspian Tern regurgitated pellets, but found no egg shells. On the other hand, Vermeer (1973) found that 3.2% of Caspian Tern pellets contained tern egg shells. I observed Caspian Terns pick up and shake egg shell fragments of egg remains after hatching or predation by gulls. Accidental ingestion on such occasions could explain a low incidence of egg shells in regurgitated pellets. I observed no damage to intact eggs by Caspian Terns. Egg damage by Ring-billed Gulls was probably the main cause of egg failure in both years of this study (Table 3).

THE CHICKS

Food Type and Availability

Rainbow Smelt, Rock Bass, Smallmouth Bass and Alewife were the prey species most frequently fed to Caspian Tern chicks (Fig. 4). All food items fed to chicks, in my study, were fish (except a lone crayfish; Cambarus spp.). Caspian Terns in Finland (Koli and Soikkeli 1974) and in the Great Lakes (Ludwig 1965, Allen 1977) reportedly fed on fish only. Vermeer (1973) analyzed regurgitated pellets of Caspian Terns from Lake Winnepeg and found 100% contained fish scales and bones, 6% contained insects, 3.2% contained egg shells and 0.3% contained bird bones. Barger (1964) reported mollusks, bird eggs, small fish, and other small aquatic organisms as Caspian Tern food items, however, no data were presented.

Alewifes were fed to chicks only sporadically and less frequently than Rainbow Smelts or Rock Bass (Fig. 4). Ludwig (1965) reported that Alewifes made up about 75% of fish found in the stomachs of 22 Great Lakes Caspian Terns. Alewifes were the most frequent food item for Caspian Tern chicks in Lake Michigan (57%, Shugart et al. 1978) and

adults in Lake Ontario (45 to 50%, Allen 1977). Ludwig (1965) attributed a recent (1953-1964) increase in the Great Lakes Caspian Tern population to an invasion of Alewifes into the Great Lakes, and subsequent Alewife population increase. Alewifes were apparently in short supply in the South Limestone Islands area in 1978 and 1979 (assuming the Alewife sampling effort by Caspian Terns was similar throughout the Great Lakes). However, since Alewifes eat Rainbow Smelt eggs, decreasing Alewife populations might have led to an increase in Rainbow Smelt populations (see Smith 1970).

The mean weight of prey items fed to chicks in my study generally increased with chick age (Table 7). Rainbow Smelt were fed proportionately more often to very young chicks, whereas Rock Bass (a larger fish species) became an important item fed to older chicks (11 days +; Fig. 4). All clearly seen feedings were included in Figures 4, 5 and 6 (including those to chicks from nests initiated late in the season). Differences between food types fed to chicks according to season (Figs. 5, 6) and according to chick age (Fig. 4) suggest that Rock Bass were fed to older chicks independent of the time of season. Although there were young chicks being fed after 22 June, when Rock Bass became an important food type (Figs. 5, 6), chicks younger than 11 days old were not fed Rock Bass (Fig. 4).

Most foraging by Caspian Terns in my study occurred out of sight of the South Limestone Islands. Soikkeli (1973b) provided evidence suggesting that Caspian Terns in Finland forage up to 70 km from the colony. It was probably advantageous for adults to carry larger fish back to the colony when chicks became large enough to eat such prey efficiently. Efficient transfer of appropriate sized fish from parent to chick

probably reduced the chance of kleptoparasitism by gulls or other terns. It seems probable that larger prey were less expensive energetically (on a weight or caloric content per prey item-foraging distance basis) than smaller prey.

My results were inconsistent with Koli and Soikkeli's (1974) conclusion that adult Caspian Terns and their chicks eat food items of the same size throughout the nesting period. Their conclusion was based on a comparison of regurgitated pellets cast during the incubation and chick feeding periods. At South Limestone Islands, however, I never saw small pellets in the colony, nor did I see Caspian Tern chicks regurgitating any pellets. Spaans (1971) found no fish-bones in pellets regurgitated by Herring Gull chicks, that had been eating fish, and concluded the bones were digested by strong stomach acid of the chicks. This appears to be the case for Caspian Terns and Koli and Soikkeli's (1974) conclusions may be unfounded.

Chick Feeding 1978 versus 1979

The maximum estimated chick feeding rate (based on time-lapse films of three nests each year) was greater in 1978 than 1979 (Table 4). Weather conditions during the periods of filming were quite similar for the two years except for more rain and one day with fog in the 1978 sample (Fig. 5). Feeding young chicks ($\leq$7 days old) usually took at least 10 sec and was likely to be caught on film (one frame per 10 sec). Cues used to establish a scored "feeding visit" were: 1) parent seen carrying a fish, 2) parent in a posture suggesting chick feeding, 3) parent in a position that would suggest chick feeding prior to brooding. This method for scoring probably resulted in an inflation of the maximum

estimated feeding rate over the actual feeding rate since parents sometimes behaved as though feeding a chick (e.g., in posture or position in the film record) when in fact, no feeding occurred. I assume that the relationship between maximum estimated feeding rates and actual feeding rates was approximately the same both years.

Caspian Tern chicks fledged at an earlier age in 1978 than 1979 on South Limestone Islands. Hudson (1979) reported that Puffin (Fratercula arctica) chicks fed additional food did not fledge earlier or at a heavier weight than controls, however, other authors suggested that food availability and weather conditions affect chick growth rates and fledging ages. Swifts and other aerial insectivores experience delayed fledging under periods of reduced food availability (O'Connor 1978). Herring Gull chicks in colonies farther removed from food sources grow more slowly than those in colonies near food sources (Hunt 1972). Arctic Tern chicks lose weight during periods of unfavorable weather (Hawksley 1957). Greater maximum estimated feeding rates, and lower fledging ages in 1978 suggest that 1978 was a better year in terms of food availability than 1979, for the South Limestone Islands Caspian Terns.

Intra-brood Food Apportionment and Sibling Competition

Caspian Terns fed A-chicks at a higher rate than B-chicks in both years of my study (Figs. 8, 9). Differences in feeding rates according to hatching order are based on both parent and chick behaviors during feedings. Casual observations both years, and culmen length measurements in 1979 (Table 9) revealed differences in chick size suggesting that (other things being equal) A-chicks were better at intra-brood feeding competition. The basis for size differences according to hatching order

was hatching asynchrony. Early hatching members of a clutch grow faster than those hatching late, in many species (e.g., European Sparrow Hawks, Moss 1979; Marsh Hawks, Picozzi 1980; Common Terns, Langham 1972; Red-winged Blackbirds, Strehl 1978; Little Blue Herons, Egretta caerulea, Werschkul 1979).

The disparity of feeding rates to A and B-chicks in my study was greater during 1979 than 1978 (Figs. 8, 9). Environmental unpredictability within and between years selects for parental mechanisms, such as asynchronous hatching, to achieve a more optimal resource distribution among offspring (Brockelman 1975). In my study, the relatively high food availability in 1978 allowed a more equal distribution of food among brood members, which led to more pairs fledging both chicks in 1978 than 1979. Presumably, in 1979, a more equal distribution of food within most broods would have reduced the survival probabilities of A-chicks and lowered the parents' reproductive success. This is because, as A-chick survival decreases, the chance of total nest failure increases.

When food was relatively abundant, in 1978, there was a correlation between feeding rate (to the brood) and the proportion fed to the least-fed chick in the brood (Table 7). Thus,as feeding rates increased, the distribution of food between A and B-chicks became more equalized. I was unable to determine conclusively whether this was a result of satiation of one chick and a subsequent increased feeding rate to the sibling (in broods receiving high feeding rates), or parental control over which chick was fed, or both. Presumably, at any point in time, the nutritional requirements of one chick are greater than those of other brood members. Because of asynchronous hatching and resultant body size differences, A-chicks probably have greater metabolic requirements than younger

siblings (at least at an early age). Sooty Tern (Sterna fuscata) chicks' metabolic rates increase with body size until 40% of the adult weight is attained, usually within the first week or 10 days (Ricklefs 1974). Assuming selfish behavior by A-chicks and passive delivery of food by parents, A-chicks should outcompete their smaller B-siblings and consume more of the food presented. Because this was not always the case in my study (Table 8), it is possible that in some broods parents fed B-chicks preferentially (especially age 0-5 days in 1978; Table 8). Such preferential feeding should reduce the size difference between chicks and decrease the competitive advantage of the A-chick. This in turn could benefit those parents capable of raising two chicks under the prevailing environmental conditions. Furthermore, the timing of preferential feeding might be important because it must be more difficult to control feedings after chicks become mobile.

In any case, as feeding rates increase (above some minimal level) the nutritional requirements of the least-fed chick are more likely to be provided as the well-fed sibling approaches satiation. Satiation of captive Caspian Tern chicks required less food when feeding rates were higher (Bergman 1956).

The importance of chick-parent communication in determining feeding rates (to broods) has been shown previously (Henderson 1975, Miller 1975). Henderson (1975) found that food deprived Glaucous-winged Gull chicks increased their rates of pecking at the parent's bill, their calling rates, and the loudness of calling. Miller (1975) reported that devocalized Ring-billed Gull chicks were fed at lower rates than control chicks

Werschkul (1979) manipulated clutches of Little Blue Herons to form broods of equal sized chicks. The growth of chicks in manipulated broods of three and four chicks were not significantly different from the growth rates of older chicks in normal broods (i.e., broods that hatched asynchronously). He concluded that the ability of parents to distribute food equally among nestlings, not the amount of food delivered, limited the growth of chicks that hatched late relative to the rest of the brood (Werschkul 1979). Especially when parental control over food distribution within broods is limited, asynchronous hatching and resultant competitive advantages of early hatching chicks is important for raising some viable offspring when food is in short supply (Lack 1954). When parental control over food distribution within broods is great, as it may be in Caspian Terns, asynchronous hatching may augment that control.

While no intense sibling aggression was noted in my study, many studies of sibling competition have found aggression. A-chicks of some raptor species reduce intra-brood feeding competition by attacking and intimidating their younger sibling(s) (e.g., Black Eagles, Ictinaetus mayayensis, Gargett 1978; Osprey, Pandion haliaetus, Poole 1979). Ingram (1959) presented circumstantial evidence suggesting that cannibalism and sibling scavenging in various birds of prey is common. Short-eared Owls (Asio flammeus) reduced sibling cannibalism by leaving surplus food within reach of the nest (Ingram 1959). The outcome of sibling aggression may be influenced by: 1) the hatching interval; 2) the feeding rate (as feeding rate increases, the tendency for aggression decreases and the ability to withstand attack increases); and 3) the amount of time chicks are left unbrooded (Newton 1977). Intense sibling

aggression was reported in MacCormick's Skuas (Stercorarius maccormicki; Procter 1975, Young 1978) and Sandhill Cranes (Grus canadensis, Miller 1973). Proctor (1975) showed experimentally that sibling aggression was regulated by hunger. Weight and age differences between siblings did not affect the ability of older MacCormick's Skua chicks to dominate their younger siblings (Procter 1975). Because even temporary food deprivation induced sibling aggression (Procter 1975), MacCormick's Skuas in areas of food availability sufficient to raise two chicks may raise both by spatially separating them, thus eliminating sibling aggression. Sandhill Cranes may have a similar solution for sibling aggression associated with temporary food shortages (see Harvey et al. 1968).

In Caspian Terns, parental control over feedings to chicks, combined with the monopolizability of discrete food items probably contributes to the lack of sibling aggression.

Chick Fates

Based on autopsies (Appendix, Table II) it appears that most chick mortality (67.2%; empty stomachs, and no apparent injury) in this study resulted from starvation or malnutrition. Some chicks with apparent external injury (23%) may actually have died from starvation or malnutrition since some external damage to chicks may have been incurred after death. Fish flesh was found in only 3% (n=2) of those chicks found dead, and one of those chicks was found stuck in vegetation. Most chicks with some stomach contents (13 of 15) had only fish bones and scales (Appendix, Table II). Spaans (1971) opened 38 freshly killed Herring Gull chicks and found that six (15.8%) had empty stomachs while the rest contained fish. Chicks autopsied in my study were not all freshly dead. I assume that fish bones were not digested after death because avian stomach acid secretion is an active process,

controlled by vagus nerves and gastrin (Prosser 1973). Furthermore three partially rotted chicks contained fish bones and one contained fish flesh (Appendix, Table II). Similarly, in Finland, autopsy showed that eight of nine Caspian Tern chicks (that died at ages 3-7 days) were in poor to very poor nutritional condition (Soikkeli 1973a). Sustained stormy weather apparently resulted in Sandwich Tern chick starvation (Veen 1977).

More B-chicks than A-chicks were found dead both years in my study (not quite statistically significant in 1979). Significantly more A-chicks died in 1979, the year of relatively low food availability, than in 1978, while B-chicks died at the same rate both years. Food-related deaths have been reported more common for chicks hatching late within a brood in common Terns, Arctic Terns, Roseate Terns, Sandwich Terns (Langham 1972), Herring Gulls (Parsons 1970), Little Blue Herons (Werschkul 1979), Snowly Egrets (Egretta thula, Raye and Burger 1979), European Sparrow Hawks (Moss 1979), some eagle species (Meyburg 1974), and Red-winged Blackbirds (Strehl 1978).

Many chicks disappeared from my study colony both years, and the likely cause of disappearance was gull predation. Ring-billed Gulls and to a lesser extent, Herring Gulls were observed preying upon Caspian Tern chicks. Since regular nest checks were thorough and fencing was effective, disappearances could be attributed to predation or scavenging. Film analysis (Appendix, Table III) suggested that diurnal scavenging was infrequent, apparently responsible for the disappearance of only one of 15 chicks that disappeared (of those analyzed; Appendix Table III). Ring-billed Gulls engaged in scavenging fish (discarded by Caspian Terns) and in one case a dead Caspian Tern chick, moved

slowly. Such gulls should have been visable on film. Chick predation, on the other hand, took about one to three seconds and could be missed easily in the photographic record. Also, some disappearances may have occurred at night. Nocturnal predation on Common Terns by Great Horned Owls (Bubo virginianus, Nisbet 1975) and Black-crowned Night-herons (Nycticorax nycticorax, Hunter and Morris 1976) have been reported.

Predation of chicks plays an important role in the breeding success of various larid species (e.g., Parsons 1975b, Davis and Dunn 1976, Fuchs 1977, Graham 1978, Shugart et al. 1978). Soikkeli (1973a) found no evidence suggesting predation of Caspian Tern chicks in Finland. However, his study involved short duration, rather infrequent colony visits in which fledging rates were estimated as the number of chicks hatched, minus the number of chicks found dead. Shugart et al. (1978) reported that Ring-billed Gull predation of Caspian Tern chicks occurred only during disturbances when adult terns were off their nests. Their observations were in contrast with mine, however, there were other apparent differences between the colonies studied. The close proximity of the food supply as well as reduced chick begging at Hat Island, Lake Michigan (Shugart et al. 1978, and G. Shugart Pers. Comm.) compared with South Limestone Islands, suggests food availability differences. A more abundant and nearby food supply presumably resulted in a greater number of unoccupied adults (because of foraging time reductions) at the colony, hence better protection from predation (see Yom Tov 1974).

Caspian Tern chicks on South Limestone Islands disappeared more frequently in 1979, the year of relatively low food availability. Reduced food availability could have resulted in increased time spent foraging by parents, reduced growth rates of chicks and associated

behavioral differences (a possible consequence of hunger). Also, if food availability was low in 1979, for the gulls on South Limestone Islands, Caspian Tern chicks may have been relatively more valuable as food items for gulls. Both Ring-billed Gulls (Chudzik 1978) and Herring Gulls (Graham 1978) fed their chicks proportionately large number of Alewifes and Rainbow Smelts which may have been less available in 1979.

A number of studies found a negative relationship between growth rates and/or food availability and chick loss by predators or aggressive conspecific neighbors. Hunt and McLoon (1975) showed that Glaucous-winged Gull chicks wandered farther from their parents after unsuccessful begging. Also, those chicks with low growth rates were more frequently killed by neighboring adults (Hunt and McLoon 1975, Hunt and Hunt 1976). Conspecific chick killing in Dominican Gulls (Laurus dominicus) correlated negatively with food availability (Fordham 1970). Since most Dominican Gull chicks were not eaten (Fordham 1970), differences in parental behavior (resulting in reduced offspring protection), and/or chick behavior were probably responsible for differences in chick killing frequencies. Evans (1970) showed that food-deprived Black-billed Gull (Larus bolleri) chicks approached non-parental mew-calls from a loudspeaker more rapidly than did parent-fed control chicks. Nisbet (1975) reported that predators consistently preyed upon Common Tern chicks of smaller than average size. Parental protection of chicks can be important in reducing predation rates. Provisioning experimental crow (Corvus corone) pairs with extra food resulted in decreased predation at those nests, apparently because of increased time spent at the nest by those parents (Yom Tov 1974).

Hungry Caspian Tern chicks, on South Limestone Islands, responded to fish-carrying adults (parents and others) by running towards them and/or emitting begging calls. The extremely low feeding rates to B-chicks that disappeared before age 15 days in 1979 (Fig. 17) suggests that these chicks were hungrier and smaller than average for their ages. A-chicks of those broods were also fed at a relatively low rate (Fig. 15) suggesting that their parents were relatively ineffective foragers. In 1978, disappearances of B-chicks before age 15 days was apparently unrelated to feeding rates (Figs. 11, 14).

Chick Ages and Losses

The general patterns of chick mortality according to age (Figs. 21, 22) are consistent with the food availability differences between years. In 1978, the year of greater food availability, few A-chicks died and B-chicks that died usually reached at least 10 days of age. On the other hand, in 1979, A-chicks died more frequently (than in 1978) and usually reached at least 10 days of age. B-chicks that died in 1979 usually starved during the early growth period prior to 10 days of age. Feeding rates to B-chicks that died before age 15 days, were, on average, reduced after age 3 days of age (Figs. 16, 18). This was partly due to increased apportionment in those broods (Fig. 18).

Starvation at an early age (less than one week) has been reported as a common occurrence in many species, including Common Terns (Langham 1972), Caspian Terns (Soikkeli 1973a), and Snowly Egrets (Raye and Burger 1979). Conversely, Harris and Plumb (1965) attributed deaths of young Herring Gulls and Lesser Black-backed Gulls to exposure, suggesting that starvation of young chicks is unlikely because some parents

are capable of meeting the food demands of adult-size young. O'Connor (1978) pointed out the critical importance of availability of small food items that can be eaten by young chicks. Parsons (1970) noted that delayed changes in parental behavior from incubation to chick feeding duties would result in low feeding rates to chicks, immediately after hatching. Before chicks attain thermoregulatory independence, parental brooding is necessary, thus limiting the parents' foraging time. Furthermore, species providing extensive parental care should reduce brood size at an early stage if brood reduction is necessary (Hamilton 1966, Emlen 1970). However, many parents in my study fed their B-chicks, despite an apparent inability by those parents, to raise two chicks. The timing of brood reduction should also take into account the likelihood of unanticipated deaths of older offspring. Delayed brood reduction would increase reproductive expectations in the event of accidental death or loss to predation of older offspring in a brood.

Chick disappearance patterns according to age (Figs. 21, 22) indicated that both A and B-chicks generally disappeared at earlier ages in 1979. Visual observations suggested that Ring-billed Gulls preyed upon small Caspian Tern chicks ($\leq$7 days old) while Herring Gulls preyed upon larger ($<$7 days old) chicks. In 1979, predation pressure from Ring-billed Gulls was apparently heavier than in 1978. B-chicks grew more slowly (see Table 9) and probably with greater variability than A-chicks. This resulted in a greater age range of small B-chicks available to predators compared with A-chicks.

Egg Weights and Chick Fates

A-chicks that disappeared, hatched from eggs that were significantly lighter than those producing chicks that fledged (Fig. 23, Table 11). Negative correlations between chick mortality and fresh egg weights have been described in several species, including Common Terns (Nisbet 1973), Black-headed Gulls (Larus ridibundus, Lundberg and Vaisanen 1979), Herring Gulls (Parsons 1970, Davis 1975), and European Swifts (O'Connor 1979). Ankney (1980) showed that increased egg size in Lesser Snow Geese correlated positively with an increased ability of chicks to survive long periods of starvation.

In Herring Gulls, the increased survivorship accrued to chicks hatching from large eggs was only important during the first week after hatching (Parsons 1970). Increased abilities to stave off starvation by Lesser Snow Goose chicks from large eggs diminished rapidly with chick age (Ankney 1980). House Sparrows and Blue Tits that were larger than conspecifics at hatching (and presumably as eggs), grew at faster rates for the first week, but the same effect was small and short-lived in House Martins (O'Connor 1975). In contrast, the growth rate advantage of Roseate Terns from larger eggs was maintained throughout the nestling period (Nisbet 1978).

To eliminate the confounding relationship between parental age (and hence foraging ability) and egg size, as related to chick survival, Nisbet (1978) switched clutches within Roseate and Common Tern colonies. His evidence suggests that egg size is important to chick survival, independent of parental abilities.

If the relationship between A-egg weight and chick survival, in my study, was due to differential parental quality (assuming parental quality correlates positively with A-egg weight), then B-sibling survival

should also have been related to A-egg weight. Fresh egg-weights of A or B-eggs were not related to survival of B-chicks or predation rates on B-chicks from those clutches, therefore, in my study, A-egg weight was probably correlated with A-chick survival independent of parental quality.

Egg weights or volume differences were largely a function of albumen content for Common and Roseate Terns (Nisbet 1978), Herring Gulls (Parsons 1976) and Laughing Gulls (Ricklefs et al. 1978). Ricklefs et al. (1978) found that the increased albumen content of Laughing Gull eggs resulted in chicks with higher body water content. Larger eggs apparently produce chicks with a better competitive ability and greater resistance to water loss (Ricklefs et al. 1978). Parsons (1976) found that yolk and soluble lipids were also strongly positively correlated with egg weight, indicating that egg-weight is an appropriate indication of energy available to the chick embryo. Food shortage during laying resulted in lower quality (smaller yolked) House Martin eggs, that produced lighter hatchlings (Bryant 1978b). O'Connor (1979) found that European Swifts hatching from relatively heavy eggs were larger than those hatching from relatively light eggs. The difference was not due to yolk content of chicks (O'Connor 1979). In Herring Gulls, however, an appreciable part of the weight difference in newly hatched chicks was a result of yolk retained within the chick at hatching (Parsons 1976).

I did not find a significant correlation between egg weight and culmen length soon after hatching of A- or B-chicks, although A-chicks had significantly longer culmens than B-chicks. Culmen lengths were measured within two days of hatching and some growth may have occurred

already. Culmen length may not have been strongly representative of body size at hatching because culmen length may be primarily a function of chick exit at hatching. Chick size or weight correlated positively with egg size or weight in Brown-headed Cowbirds (Molothrus ater, Nolan and Thompson 1978), Lesser Snow Geese (Ankney 1980), European Swifts (O'Connor 1979) and Herring Gulls (Parsons 1970). Considering errors in culmen length measurements in my study (associated with growth by some chicks before they were measured), it is possible that culmen length did not accurately reflect the relative sizes of chicks. From the previously mentioned literature, the most likely differences between chicks as a function of egg size (or weight) are water content, yolk sac size and body size. Yolk sac size might have an effect on the behavior of young chicks. Those lacking yolk (a food reserve) would be most likely to be in need of nutriment. Hungry chicks would be more obvious, therefore more susceptible to predators as a result of begging and associated locomotory behavior. A second possibility is that A-chicks from large eggs escaped predation by a predator that was less likely to, or capable of, successfully preying upon chicks above a certain size. Predation of young Sandwich Tern chicks by Black-headed Gulls has been reported (Fuchs 1977, Veen 1977). Peak predation occurred as chicks left the nest and B-chicks were preyed upon, whereas A-chicks, because of their size, suffered much reduced predation (Veen 1977). Hunter and Morris (1976) reported nocturnal predation of numerous 1-2 day old Common Terns by a Black-crowned Night-Heron.

Smaller sized Caspian Tern chicks from my study may have been a more suitable prey for predators such as Ring-billed Gulls. All observations of Ring-billed Gull predation on Caspian Tern chicks involved

small chicks that could fit (except for the legs) within the crop and bill of the predator. Ring-billed Gull predators never, in my observation, lost these chick prey to other gulls, whereas those Ring-billed Gulls seen carrying exposed items such as unswallowed fish or Red-winged Blackbird adults were chased by conspecifics and often lost their prey (Pers. obs.). Possibly the risks of kleptoparasitism reduced the probable benefits of preying upon larger chicks to a point below the probable costs. This hypothesis does not imply that A-egg weight is necessarily an adaptation to a size restricted predator (see Williams 1966). It may simply reflect an adaptation maximizing the success of asynchronous hatching favoring brood reduction when necessary, hence smaller B-eggs.

Fledging Success

Fledging success in my study varied with hatching order and yearly food availability. Apparently, increased food availability allowed better parental care in 1978 and may have promoted increased reproductive effort (see Gadgil and Bossert 1970). Fledging success rates reported here are within the range reported by Shugart et al. (1978), although some of their colonies were highly disturbed (G. Shugart Pers. Comm.)

Three-egg clutches produced more fledged chicks per nest than did the modal clutch size of 2-eggs (Table 15), although the difference was not significant. Since no C-chicks fledged either year, the difference was based on A- and B-chick fledging success. The presence of C-chicks may have reduced thermoregulatory costs to A- and B-chicks (see Mertens 1969, Royama 1969). Langham (1972) reported better fledging success by pairs of Common Terns with relatively large clutches. It is possible that older birds laid larger clutches and increased reproductive effort

in response to decreasing reproductive value (Pianka and Parker 1975, Stearns 1976), and increased parental experience. Robertson and Biermann (1979) showed that Red-winged Blackbird parental investment (chick feeding and nest defense) in the whole clutch or brood increased as a function of manipulated clutch size. Thus, increased parental efforts and subsequent success may be a function of expected benefits.

The fledging success of 1-egg clutches in my study was misleading on a per nest basis. On a per chick basis, 1-egg clutches did best both years (Table 15), although the differences were not significant (possibly due to small sample sizes). Fresh eggs from 1-egg clutches were significantly lighter in weight than A-eggs of 2-egg clutches, suggesting that these may have been produced by younger parents (see Parsons 1972, Davis 1975, Ryder 1975, Coulson and Horubin 1976, Mills 1979). Soikkeli (1973a) did not find any dead Caspian Tern chicks of 1-chick broods in Finland. Apparently most Caspian Terns, in these studies, that hatched one egg were capable of fledging one chick.

In 1979, 2-egg clutches initiated early in the season generally fledged more chicks than did later initiated 2-egg clutches. The difference was not significant, however, this analysis was based on study nests only, excluding late nesting pairs. The trend may reflect earlier laying by older and more experienced birds, or a reduction in food availability (or randomness). Kirkham and Morris (1979) suggested that for Ring-billed Gulls in a Lake Ontario colony, the coincident timing of peak hatching and peak availability of aerial insects probably represented a synchronization of breeding activity and seasonal availability of aerial insect food. Differences in fledging success according to clutch initiation dates have also been attributed to

parental age differences (Coulson 1966, Morris and Haymes 1977).

In my study relatively large hatching intervals did not preclude the fledging of two chicks (Table 14). Despite evidence that Common Terns capable of raising three chicks increased within-brood hatching synchrony (Nisbet and Cohen 1975), the mean hatching interval was greater in pairs fledging both A- and B-chicks in my study (Table 14). In clutches of parents that were unable to raise two chicks, B-chick success was apparently more likely if the hatching interval had been small (Table 14). This may have been a result of increased competitive abilities of those B-chicks (A-chicks had less of a head start) and a greater likelihood of being fledged if the A-chick died.

Some proximate factors are involved in determination of the degree of within-brood hatching synchrony. Hatching intervals within Common Tern broods were significantly correlated with laying dates (Nisbet and Cohen 1975). This in turn may be related to parental age (e.g., Coulson and White 1958). Differences in fledging success according to hatching interval were probably not due to the hatching interval alone.

Parent-Offspring Conflict

Both years of my study, parents that hatched both A- and B-eggs had, on average, the best fledging per pair success (Table 12). A-chicks did equally well whether or not their B-siblings hatched, however, B-chicks of clutches from which A-eggs failed to hatch, fledged significantly more frequently, both years, than those with A-siblings that did hatch (Table 12).

Under certain conditions, natural selection acting on parents and chicks creates a conflict of interest (Trivers 1974, Alexander 1974).

Assuming single paternity, chicks within a brood are of equal genetic value to their parents (i.e., all related by one-half). Each chick is related to itself by one and to a sibling by only one-half. Based on inclusive fitness theory (Hamilton 1964) it may pay chicks to behave selfishly, contrary to the reproductive interests of the parents. There must be a risk to older chicks when parents attempt to raise the whole brood when food is limiting. If so, chicks theoretically should behave selfishly whenever the cost of behaving otherwise is not at least doubled by the benefits (costs and benefits both measured in future reproductive success) accrued to siblings (Hamilton 1964). Trivers (1974) suggested that psychological manipulation of parents by offspring mustbe an effective weapon, however, Alexander (1974) maintained that parents would in most cases have the greatest control.

My data suggest that early in the chick feeding period (age 0-10 days of B-chicks) food apportionment was adjusted to the feeding rate when sufficient food was available (i.e., in 1978, Table 7). The choice of chick fed was probably determined by the chicks' behavior (based in part on the nutritional state of each chick) and to some degree on the parents' behavior (as discussed previously). Increased mobility by chicks may have resulted in reduced parental control over which chick was fed, however, most chick losses occurred by age 10 days (Figs. 21, 22), therefore, parental control was maintained during the critical period.

Using inclusive fitness considerations, O'Connor (1978) investigated the literature addressing brood reduction in birds. He suggested that parents, victims (those chicks eliminated by brood reduction) and survivors (those chicks surviving after brood reduction) should have

different thresholds (based on inclusive fitness) for promoting brood reduction. Survivors should have the lowest threshold for promoting brood reduction, parents should be intermediate and finally the victims should have the highest threshold. Asymmetries in thresholds for the promotion of brood reduction theoretically induces first fratricide by the survivors, then infanticide (direct or through starvation) by parents, and finally suicide by victims as food becomes increasingly limited (O'Connor (1978) O'Connor's (1978) evidence was admittedly speculative.

Because of asynchronous hatching and subsequent differences in competitive ability, the only potential for parent-offspring conflict involving direct physical interference in two-chick broods, from my study, was between parents and A-chicks. Conflicts between parents and B-chicks would be more subtle, for example, exaggerated parental solicitation by B-chicks.

MacNair and Parker (1979) modelled parent-offspring conflict situations involving parental solicitation by offspring and parental food apportionment within a brood. When parental retaliation is not allowed, "selfish" genes coding for exaggerated begging, presumably "little lies" (see Otte 1974), can spread in a population (MacNair and Parker 1979). The result is reduced parental fitness relative to pairs with non-exaggerating chicks. When parental retaliation was allowed (Parker and McNair 1979), the most likely result involved evolutionary stable strategies (Maynard Smith and Price 1973) with parents providing more food than would be optimal in absence of the conflict, but less than optimal for the exaggerating chick(s).

The genome best suited to parent-offspring conflict appears to be one of optimal compromise between parent and offspring interests. The degree of compromise at each level depends on the relative selection pressures, because the gene complex best suited for leaving reproductive offspring and other relatives sharing those genes (e.g., siblings) will be promoted throgh natural selection.

My data do not allow an assessment of subtle parent-offspring conflict (e.g., exaggerated begging). Direct interference (sibling competition) during chick feeding by B-chicks is unlikely considering the size difference between A- and B-chicks. While A-chicks were larger, hence better at intra-brood feeding competition (recall that presence or absence of a hatched B-sibling did not affect A-chick fledging success), there is some evidence of suggesting parental control over which chick was fed (prior to age 10 days B-chick age) in some broods (see Table 8). Despite apparent parental control of food apportionment within some broods, A-chicks generally received more parental investment than did B-chicks. This appears to be consistent with parent-offspring conflict, however, A-chicks are probably more valuable to parents than are B-chicks in terms of survival probability and amount of future required parental investment (see Dawkins and Carlisle 1976). Thus, no conclusive evidence was presented demonstrating parent-offspring conflict in this study, perhaps owing to difficulties in assessing the subtleties of its expression. Furthermore, as parental experience increases, competence in parental decision making and the ability to avoid psychological manipulation by offspring should increase. If these effects of experience coincide with increased foraging competence (see Orians 1969, Recher and Recher 1969, Dunn 1972, Buckley and Buckly 1974,

Verbeek 1977, Searcy 1978) and increased likelihood of raising a full brood, as well as abilities to control food apportionment, then parent-offspring conflict may be slight. Theoretically, conflict should be greatest between inexperienced parents and their older chicks, when delays of brood reduction (as insurance against older chick loss) are potentially costly to older chicks.

Parental Investment and Brood Reduction

Differential investment in eggs, combined with the effects of asynchronous hatching, produced a linear hierarchy of chick sizes in my study. This hierarchy, in turn, facilitated brood reduction when food was insufficient for the successful raising of two chicks. Differential food availability and differential apportionment of food between the 1978 and 1979 seasons were reflected in the contrasting number of pairs that fledged two chicks each year. While some pairs, both years, were able to raise two chicks, effectively doubling their potential reproductive success that season, other pairs apparently concentrated their parental investment into A-chicks (especially in 1979). B-chicks in those broods may have been relegated to the status of "insurance" against early losses of A-chicks. However, B-chicks that eventually died were fed a considerable portion of food at an early age. Theoretically, feeding B-chicks that will likely die (unless the A-chick dies) should continue until the cost of doing so outweighs the benefits. Costs would be measured as the probability of reduced reproductive success through lowering the A-chicks fitness. Benefits would be measured as the probability of increased reproductive success through raising the B-chicks fitness (e.g., 1) in case of non-food related A-chick mortality

or 2) in case of a sudden increase in food availability allowing successful rearing of two chicks).

Concentrated parental investment in A-chicks was probably best for pairs marginally, or less capable of raising two chicks under existing conditions since offspring quality is important to reproductive success (Brockelman 1975). In Caspian Terns, the post-fledging period is critical, and chick quality at fledging is important. Post-fledging and pre-adult mortality rates were estimated, from band returns, at 62% of all mortalities (Ludwig 1965). High mortality rates of young (fledged) Caspian Terns are probably, in part, because of the high degrees of skill required for their feeding behavior. It is probably for this reason that parental care extends at least until the migration period of the first year (Jozefik 1969).

The concept of "insurance eggs" was used with reference to two species of boobies (Sula dactyla and S. leucogaster) that were only capable of raising one chick, but regularly laid two eggs (Dorward 1962). This is a likely function of B-eggs and chicks in many raptor species (see Meybur 1974, Newton 1974).

Appropriate apportionment of parental investment within clutches and broods of Caspian Terns allowed successful fledging of A- and B-chicks by some parents and effective brood reduction allowing successful fledging of one (usually A-) chick by others. Presumably, this flexibility allows maximization of the lifelong reproductive success of individual Caspian Terns.

LITERATURE CITED

Alexander, R.D. 1974. The Evolution of social behavior. Annual Review of Ecology and Systematics 5: 325-383.

Allen, L.J. The comparative feeding ecology relative to population dynamics of the Herring and Ring-billed Gulls (Larus argentatus and L. delawarensis) and some comparisons with the Caspian Tern. Kingston, Ontario: Queen's University; 1977. MSc Thesis.

Amadon, Dean. 1964. The evolution of low reproductive rates in birds. Evolution 18:105-110.

Andersson, M. 1977. Natural selection of offspring numbers: some possible intergeneration effects. Amer. Natur. 111:762-766.

Ankney, C.D. 1980. Egg Weight, survival, and growth of lesser snow goose goslings. J. Wildl. Manage.:44:174-182.

Askenmo, C. 1977. Effects of addition and removal of nestlings on nestling weight, nestling survival and female weight loss in the Pied Flycatcher Ficedula hypoleuca (Pallas). Ornis. Scand. 8:1-8.

Barger, N.R. 1964. Caspian Tern Hydroprogne caspia imperator (identification habits diet). Wisconsin Conservation Bulletin 29:30.

Bergman, G. 1953. Verhalten und Biologie der Raubseeschwalben (Hydroprogne tschegrava). Acta Zool. Fennica 77:1-50.

_____. 1956. On the development of behavior in chicks of the Caspian Tern. Var Fagelevard 15:223-245.

Blus, L.J., and J.A. Keahey. 1978. Variation in reproduction with age in the Brown Pelican. Auk 95:128-134.

Brockelman, W.Y. 1975. Competition, the fitness of offspring and optimal clutch size. Amer. Natur. 109:677-699.

Bryant, D.M. 1975. Breeding biology of House Martins Delichon urbica in relation to aerial insect abundance. Ibis 117:180-216.

_____. 1978a. Establishment of weight hierarchies in the broods of House Martins Delichon urbica. Ibis 120:16-26.

_____. 1978b. Environmental influence on growth and survival of nestling House Martins Delichon urbica. Ibis 120:271-283.

Buckley, F.G. and P.A. Buckley. 1972. The breeding ecology of Royal Terns, Sterna (Thalasseus) Maxima Maxima. Ibis 114:344-359.

_____. 1974. Comparative feeding ecology of wintering adult and juvenile Royal Terns (Aves:Laridae, Sterninae). Ecology 55:1053-1063.

Charnov, E.L. and J.R. Krebs. 1974. On Clutch-size and fitness. Ibis 116:217-219.

Chudzik, J. Reproductive success and chick feeding ecology of Ring-billed Gulls Larus delawarensis, on South Limestone Island. St. Catharines, Ontario: Brock University; 1978. BSc. thesis.

Cody, M.L. 1966. A general theory of clutch size. Evolution 20:174-184.

_____. Ecological aspects of reproduction. Farner D.S. and J.R. King eds. Avian Biology. Vol. 1 New York: Academic Press; 1971.

Coulson, J.C. 1966. The influence of the pair bond and age on the breeding biology of the Kittiwake gull Rissa tridactyla. J. Anim. Ecol. 35:269-279.

Coulson, J.C. and J. Horubin. 1976. The influence of age on the breeding biology and survival of the Arctic Tern Sterna paradisaea. J. Zool. 178:247-260.

Coulson, J.C., and C. Thomas. 1978. The significance of egg size in gulls. Ibis 120:407.

Coulson, J.C., and E. White. 1958. The effect of age on the breeding biology of the Kittiwake Rissa tridactyla. Ibis 100:40-51.

_____. 1961. An analysis of the factors influencing the clutch size of the Kittiwake. Proc. Zool. Soc. London 136:207-217.

Cronmiller, J.R., and C.F. Thompson. 1980. Experimental Manipulation of brood size in Red-winged Blackbirds. Auk 97:559-565.

Darwin, C. The descent of man and selection in relation to sex. London: John Murray; 1871.

Davis, J.W.F. 1975. Age, egg-size and breeding success in Herring Gulls (Larus argentatus). Ibis 117:460-473.

_____. 1976. Breeding success and experience in the Arctic Skua, Stercorarius parasiticus (L.). J. Anim. Ecol. 45:531-535.

Davis, J.W.F., and E.K. Dunn. 1976. Intraspecific predation and colonial breeding in lesser Black-backed Gulls Larus fuscus. Ibis 118:65-77.

Dawkins, R. The selfish gene. Oxford: Oxford University.Press; 1976.

Dawkins, R. and T.R. Carlisle. 1976. Parental investment, mate desertion and a fallacy. Nature 262:131-133.

DeGroot, D.S. 1931. History of a Nesting Colony of Caspian Terns on on San Francisco Bay. Condor 33:188-192.

De Steven, D. 1980. Clutch size, breeding success, and parental survival in the tree swallow (Iridoprocne bicolor) Evolution 34:278-291.

Dorward, D.F. 1962. Comparative biology of the White Booby and the Brown Booby Sula spp. at Ascension. Ibis 103b:174-220.

Dunn, E.K. 1972. Effect of age on the fishing ability of Sandwich Terns Sterna sandvicensis. Ibis 114:360-366.

_____. 1975. The role of environmental factors in the growth of tern chicks. J. Anim. Ecol. 44:743-754.

Emlen, J.M. 1970. Age specificity and ecological theory. Ecology 51: 588-601.

Emlen, S.T., and L.W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197:215-223.

Evans, R.M. 1970. Parental recognition and the mew call in Black-billed Gulls (Larus bulleri). Auk 87:503-513.

Evans, Roger J., David B. Krindle and Mark E. Mattson. 1970. Caspian Terns nesting near Spruce Island Lake Winnipegosis Manitoba. Blue Jay 28:68-71.

Evans, R.M. and M.K. McNicholl. 1972. Variations in the reproductive activities of Arctic Terns at Churchill Manitoba, Arctic 25:131-141.

Fisher, R.A. The genetical theory of natural selection. New York: Dover Publications; 1958.

Fordham, R.A. 1970. Mortality and population change of Dominican Gulls in Wellington New Zealand. J. Anim. Ecol. 39:13-27.

Fuchs, E. 1977. Predation and anti-predator behavior in a mixed colony of terns Sterna sp. and Black-headed Gulls Larus ribibundus with special reference to the Sandwich Tern Sterna sandvicensis. Ornis. Scand. 8:17-32.

Gadgil, M., and W.H. Bossert. 1970. Life historical consequences of natural selection. Amer. Natur. 104:1-24.

Gargett, V. 1978. Sibling aggression in the Black Eagle in the Matopos Rhodesia. Ostrich 49:57-63.

Gillet, W.H., J.L. Hayward, Jr., and J.F. Stout. 1975. Effects of human activity on egg and chick mortality in a Glaucous-winged Gull colony. Condor 77:492-495.

Goodman, D. 1974. Natural selection and a cost ceiling on reproductive effort. Amer. Natur. 108:247-268.

Graham, K.D. Reproductive parameters and chick feeding ecology of the Herring Gull (Larus argentato with comparisons to cohabiting Ring-billed Gulls (Larus delawarensis) on South Limestone Island. St. Catharines, Ontario: Brock University; 1978. BSc. thesis.

Hamilton, W.D. 1963. The evolution of altruistic behavior. The Amer. Natur. 97:354-356.

_____. 1964. The genetical theory of social behavior I, II. J. Theor. Biol. 7:1-52.

_____. 1966. The moulding of senescence by natural selection. J. Theoret. Biol. 12:12-45.

Harris, M.P. 1969. Food as a factor controlling the breeding of Puffinus Ihermineri. Ibis 111:139-156.

Harris, M.P., and W.J. Plumb. 1965. Experiments on the ability of Herring Gulls Larus argentatus and Lesser Black-backed Gulls L. fuscus to raise larger than normal broods. Ibis 107:256-257.

Harvey, J.M., B.C. Lieff, C.D. MacInnes, and J.P. Prevett. 1968. Observations on behavior of Sandhill Cranes. Wilson Bull. 80: 421-425.

Hawksley, O. 1957. Ecology of a breeding population of Arctic Terns. Bird Banding 28:57-92.

Haymes, G.T., and R.D. Morris. 1977. Brood size manipulation in Herring Gulls. Can. J. Zool. 55:1762-1766.

Henderson, B.A. 1975. Role of the chick's begging behavior in the regulation of parental feeding behavior of Larus glaucescens. Condor 77:488-492.

Hudson, P.J. 1979. The parent-chick feeding relationship of the Puffin Fratercula arctica. J. Anim. Ecol. 48:889-898.

Hunt, G.L. 1972. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. Ecology 53:1051-1061.

Hunt, G.L., and M.W. Hunt. 1976. Gull chick survival: The significance of growth-rates, timing of breeding, and territory size. Ecology 57:62-75.

Hunt, G.J., Jr., and S.C. McLoon. 1975. Activity patterns of Gull chicks in relation to feeding by parents: their potential significance for density dependent mortality. Auk 92:523-527.

Hunter, R.A., and R.D. Morris. 1976. Nocturnal predation by a Black-crowned Night Heron at a Common Tern colony. Auk 93:629-633.

Ingram, C. 1959. The importance of juvenile cannibalism in the breeding biology of certain birds of prey. Auk 76:218-226.

Jozefik, Mieczyslaw. 1969. Caspian Tern, Hydropragne caspia PALL. in Poland-the biology or migration period. Acta Ornithologica 11: 381-427.

Kadlec, J.A., and W.H. Drury. 1968. Structure of the New England Herring Gull population. Ecology 49:644-676.

Kirkham, I.R., and R.D. Morris. 1979. Feeding ecology of Ring-billed Gull (Larus delawarensis) chicks. Can. J. Zool. 57:1086-1090.

Koli, L. and M. Soikkeli. 1974. Fish prey of breeding Caspian Terns in Finland. Ann. Zool. Fennici 11:304-308.

Lack, D. The natural regulation of animal numbers. London: Oxford University Press; 1954.

_____. Population studies of birds. Oxford: Clarendon Press; 1966.

_____. Ecological adaptations for breeding in birds. London: Methuen; 1968.

Langham, N.P.E. 1972. Chick survival in terns (Sterna spp.) with particular reference to Common Terns. J. Anim. Ecol. 41:385-395.

Lemmetyinen, R. 1973a. Clutch size and timing of breeding in the Arctic Tern in the Finnish archipelago. Ornis Fenn. 50:18-27.

_____. 1973b. Feeding ecology of Sterna paradisaea in the archipelago of southwestern Finland. Am. Zool. Fennici 10:507-525.

Ludwig, F.E. 1942. Migration of Caspian Terns Banded in the Great Lakes area. Bird Banding 13:1-9.

Ludwig, J.P. 1962. A survey of the Gull and Tern populations of Lakes Huron, Michigan and Superior. The Jackpine Warbler 40:104-119.

_____. 1965. Biology and Structure of the Caspian Tern (Hydroprogne caspia) population of the Great Lakes from 1894-1964. Bird Banding 36(4):217-233.

Lundberg, C.A., and R.A. Vaisanen. 1979. Selective correlation of egg size with chick mortality in the Black-headed Gull (Larus ridibundis). Condor 81:146-156.

MacNair, M.R., and G.A. Parker. 1979. Models of parent-offspring conflict. III. Intra-brood conflict. Anim. Behav. 1202-1209.

Malec, M.A. Essential statistics for social research. Philadelphia: J.B. Lippincott Co.; 1977.

Maynard Smith, J., and G.R. Price. 1973. The logic of animal conflict. Nature 246:15-18.

Mertens, J.A.L. 1969. The influence of brood size on the energy metabolism and water loss of nestling Great Tits Parus Major Major.

Meyburg, B.V. 1974. Sibling aggression and mortality among nestling eagles. Ibis 116:224-228.

Miller, A.H. 1943. Census of a colony of Caspian Terns. Condor, 45: 220:225.

Miller, D.E. 1975. Chick vocalizations as factors inducing parental feeding in the Ring-billed Gull. Am. Zool. 15:804.

Miller, R.S. 1973. The brood-size of cranes. Wilson Bull. 85:436-441.

Mills, J.A. 1973. The influence of age and pair-bond on the breeding biology of the Red-billed Gull Larus Novaehollandiae scopulinus. J. Anim. Ecol. 42:147-162.

_____. 1979. Factors affecting the egg size of Red-billed Gulls Larus novaehollendiae scopulinus. Ibis 121:53-67.

Moss, D. 1979. Growth of Nestling Sparrowhawks (Accipiter nisus). J. Zool., Lond. 187:297-314.

Nelson, J.B. 1964. Factors influencing clutch size and chick growth in the North Atlantic Gannet, Sula bassana. Ibis 106:63-77.

Newton, I. 1977. Breeding strategies in birds of prey. The Living Bird 16:51-82.

Nisbet, I.C.T. 1973. Courtship-feeding, egg-size and breeding success in Common Terns. Nature 241:141-142.

_____. 1975. Selective effects of predation in a tern colony. Condor 77:221-226.

_____. 1978. Dependence of fledging success on egg size, parental performance and egg composition in Common and Roseate Terns, Sterna hirundo and S. dougallii. Ibis 120:207-215.

Nisbet, I.C.T., and M.E. Cohen. 1975. Asynchronous hatching in Common and Roseate Terns, Sterna hirundo and S. dougallii. Ibis 117: 374-379.

Nisbet, I.C.T., and W.H. Drury. 1972. Measuring breeding success in Common and Roseate Terns. Bird Banding 43:97-106.

Nisbet, I.C.T., K.J. Wilson, and W.A. Broad. 1978. Common Terns raise young after death of their mates. Condor 80:106-109.

Nolan, V., and C.F. Thompson. 1978. Egg volume as a predictor of hatchling weight in the Brown-headed Cowbird. Wilson Bull. 90: 353-358.

O'Connor, R.J. 1975. Initial size and subsequent growth in passerine nestlings. Bird Banding 46:329-340.

_____. 1977a. Differential growth and body composition in altricial passerines. Ibis 119:147-166.

_____. 1977b. Growth strategies in nestling passerines. The Living Bird 16:209-238.

_____. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? Anim. Behav. 26:79-96.

_____. 1979. Egg weights and brood reduction in the European Swift (Apus apus). Condor 81:133-145.

O'Donaghue, C.H. and J.N. Gowanlock. 1919. Notes on the Caspian Tern (Sterna caspia) and the Parasitic Jaeger (Stercorarius parasiticus) in Manitoba Can. Field Natur. 33:1-6.

Orians, G.H. 1969. Age and hunting success in the Brown Pelican (Pelecanus occidentalis). Anim. Behav. 17:316-319.

Otte, D. 1974. Effects and functions in the evolution of signalling systems. Ann. Rev. of Ecol. and Syst. Vol. 5:385-416.

Palmer, R.S. 1941. A behavioral study of the Common Tern (Sterna hirundo hirundo L.). Proceedings of the Boston Society of Natural History 42:1-119.

Parker, G.A. and M.R. MacNair. 1979. Models of parent-offspring conflict. IV. Suppression: evolutionary retaliation by the parent. Anim. Behav. 27:1210-1235.

Parsons, J. 1970. Relationship between egg-size and post-hatching chick mortality in the Herring Gull (Larus argentatus). Nature 228: 1221-1222.

_____. 1972. Egg size, laying date, and inc. period in the Herring Gull. Ibis 114:536-541.

_____. 1975a. Asynchronous hatching and chick mortality in the Herring Gull Larus argentatus. Ibis 117:517-520.

_____. 1975b. Seasonal variation in the breeding success of the Herring Gull: an experimental approach to pre-fledging success. J. Anim. Ecol. 44:553-573.

_____. 1976. Factors determining number and size of eggs laid by Herring Gulls. Condor 78:481-497.

Penland, S. 1976. The Caspian Tern: A natural history. Washington Wildlife 28:16-19.

Perrins, C.M. The role of predation in the evolution of clutch size. Stonehouse, B. and C. Perrins eds. Evolutionary ecology. London: MacMillan; 1977.

Pianka, E.R., and W.S. Parker. 1975, Age-specific reproductive factors. Am. Nat. 109:453-464.

Picozzi, N. 1980. Food, growth, survival and sex ratio of nestling Hen Harriers Circus c. cyaneus in Orkney, Ornis Scand. 11:1-11.

Poole, A. 1979. Sibling aggression among nestling Ospreys in Florida Bay. Auk 96:415-417.

Procter, D.L.C. 1975. The problem of chick loss in the South Polar Skua Catharacta maccormicki. Ibis 117:452-459.

Prosser, C.L. Stimulation of secretion of digestive fluids. Prosser, C.L. ed. Comparative animal physiology. Toronto:W.B. Saunders Co.; 1973.

Raye, S.S.C., and J. Burger. 1979. Behavioral determinants of nestling success of Snowy Egrets (Leucophoyx thuia). American Midland Naturalist 102:76-85.

Recher, H.F. and J.A. Recher. 1969. Comparative foraging efficiency of adult and immature Little Blue Herons (Florida caerulea). Anim. Behav. 17:320-322.

Ricklefs, R.E. 1965. Brood reduction in the Curve-billed Thrasher. Condor 67:505-510.

_____. Energetics of reproduction in birds. Paynter, R.A., Jr., ed. Avian energetics. Cambridge Massachusetts: Nuttall Ornithological Club publication number 15; 1974:152-297.

Ricklefs, R.E., D.C. Hahn, and W.A. Montevecchi. 1978. The relationship between egg size and chick size in the Laughing Gull and Japanese Quail. The Auk 95:135-144.

Robertson, R.J., and G.C. Biermann. 1979. Parental investment strategies determined by expected benefits. Z. Tierpsychol. 50:124-128.

Royama, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits Parus Major. The Ibis 108:323-347.

Ryan, R.A., B.L. Joiner, and B.F. Ryan. Minitab students handbook. Massachusetts: Duxbury Press; 1976.

Ryder, J.P. 1975. Egg-laying, egg size, and success in relation to immature-mature plumage of Ring-billed Gulls. The Wilson Bull. 87(4):534-542.

Scott, W.B., and E.J. Crossman. Freshwater fishes of Canada. Bull. 184, Fisheries Research Board of Canada; 1973.

Searcy, W.A. 1978. Foraging success in three age classes of Glaucous-winged Gulls. Auk 95:586-588.

Shugart, G.W., W.C. Scharf, F.J. Cuthbert. 1978. Status and reproductive success of the Caspian Tern (Sterna caspia) in the U.S. Great Lakes. Proc. 1978 Colonial Waterbird Group:110-117.

Siegel, S. Nonparametric statistics for the behavioral sciences. Toronto:McGraw-Hill Book Co. Inc.; 1956.

Smith, S.H. 1970. Species interactions of the alewife in the Great Lakes. Trans. Amer. Fish. Soc. 4:754-765.

Soikkeli, M. 1973a. Breeding success of the Caspian Tern in Finland. Bird Banding 44:196-204.

_____. 1973b. Long-distance fishing flights of the breeding Caspian Tern. Ornis Fennica 50:47-48.

Spaans, A.L. 1971. On the feeding ecology of the Herring Gull Larus argentatus Pont. in the northern part of the Netherlands. Ardea 59: 73-188.

Stearns, S.C. 1976. Life history tactics: a review of the ideas. The Quarterly Review of Biology 51:3-47.

Strehl, C. 1978. Asynchrony of hatching in Red-winged Blackbirds and survival of late and early hatching birds. Wilson Bull. 90:653-655.

Trivers, R.L. Parental investment and sexual selection. Campbell, B. ed. Sexual selection and the descent of man, 1871-1971. Chicago: Aldine; 1972:136-179.

_____. 1974. Parent-offspring conflict. Amer. Zool. 14:249-264.

Vaisanen, R.A. 1973. Establishment of colonies of Caspian Tern Hydroprogne caspia by deserting flights in the northern Gulf of Bothnia. Ornis Scand. 4:47-53.

Veen, J. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern (Sterna S. sandwicensis Lath.). Behavior Supplement 20; 1977.

Verbeek, N.A.M. 1977. Comparative feeding behavior of immature and adult Herring Gulls. Wilson Bull. 89:415-421.

Vermeer, K. 1973. Comparisons of food habits and mercury residues of Caspian and Common Terns. Canadian Field Naturalist 34:305.

Ward, J. Factors influencing reproductive success, winter mortality, and the evolution of clutch size in the Glaucous-winged Gull. Vancouver B.C.: University of British Columbia; 1973. Dissertation.

Werschkul, D.F. 1979. Nestling mortality and the adaptive significance of early locomotion in the Little Blue Heron. Auk 96:116-130.

Williams, G.C. Adaptation and natural selection. Princeton: Princeton University Press; 1966.

Wilson, E.O. Sociobiology, Cambridge Massachusetts: The Belknap Press of Harvard University Press; 1975.

Yom-Tov, J. 1974. The effect of food and predation on breeding density and success, clutch size, and laying date of the crow (Corvus corone L.). J. Anim. Ecol. 43:479-498.

Young, E.C. 1978. Behavioural ecology of lonnbergi Skuas in relation to environment on the Chatham Islands, New Zealand. New Zealand Journal of Zoology 5:401-416.

Appendix I

The mean standard adult exposed culmen length was determined as follows: Godfrey (1966) gave a mean exposed culmen length for adult male Caspian Terns, however, no such measurement was given for adult females. Measurements of 10 male and 10 female adult Caspian Terns (by me at the American Museum of Natural History, New York, New York) collected in Texas revealed significant differences in culmen lengths (Mann Whitney U Test U1 = 26, U2 = 74, P 0.05). Male tern culmen lengths averaged 6.822 cm while females averaged 6.577 cm. The difference represented 3.59% of the male mean culmen length. To adjust Godfrey's culmen length I subtracted (3.59 ÷ 2)% of the value given. This value of 6.8154 was taken as the average culmen length of a parent Caspian Tern.

Appendix II

Clutch initiation date and hatch and fledge success:

Comparisons between early (7-11 May, n=40) and late (16-21 May, n=17) initiated 2-egg clutches from 1978 revealed no significant differences in hatching (X^2c = 0.525, $P > 0.1$) or fledging (X^2c = 0.031, $P > 0.1$) success rates. I assumed that chicks classified as "unknown" or "probably fledged" (see Table 9) actually did fledge. In 1979, early (9-17 May, n=13) and late (27-31 May, n=25) initiated 2-egg clutches did not differ significantly in hatching (X^2c = 0.647, $P > 0.1$) or fledging (X^2c = 2.928, $0.1 > P > 0.05$) success rates.

Appendix Table 1: Correlation Coefficients and Exponential Equations of Weight-Length Relationships of Prey Species, used to Estimate Weights of Prey Items Fed to Chicks

		Weight-Length Curve	
Species	Sample Size	Correlation Coefficient	Exponential Equation
Rainbow Smelt (Osmerus mordax)	60	+0.98	Log_e W* = 0.24610(L)** -0.74778
Rock Bass (Ambloplites rupestris)	37	+0.95	Log_e W = 0.73803 + 0.22723(L)
Small-mouth Bass (Micropterus dolomieui)	74	+0.99	Log W = 2.11879 + 0.13017(L)
Alewife (Alosa pseudoharengus)	58	+0.99	Log_e W = 0.25406(L) - 0.29395
Yellow Perch (Perca flavescens)	98	+0.98	Log_e W = 0.76682 + 0.18343(L)

*weight (g)

**length (cm)

Appendix Table II: Results of Autopsies Performed on Known Aged Chicks Found Dead in 1978 and 1979

Year	Hatching Order	Age When Found	External Condition	Exposed Culmen Length	Stomach Contents	Yolk	Parasites (Hirudinea)
1978	B	36	Undamaged	3.3	empty	no data	no data
1978	B	8	Undamaged	1.7	empty	no data	no data
1978	B	6	Undamaged	1.7	empty	no data	no data
1978	B	10	Undamaged	2.1	empty	no data	no data
1978	C	8	Undamaged	1.7	empty	no data	no data
1978	B	4	Undamaged	1.5	empty	no data	no data
1978	B	5	Undamaged	1.5	empty	no data	no data
1978	A	5	Skull squashed	1.4	few fish bones	no data	no data
1978	C	3	Undamaged	1.3	empty	no data	no data
1978	B	6	Undamaged	1.6	empty	no data	no data
1978	C	4	Undamaged	1.5	empty	no data	no data
1978	A	10	Undamaged	2.4	empty	no data	no data
1978	B	4	Undamaged	1.7	empty	no data	no data
1978	B	12	Undamaged	2.9	empty	no data	no data
1978	B	11	Slight damage	2.3	empty	no data	no data
1978	A	2	damage with body cuts	1.7	no data	no data	no data
1978	B	21	Undamaged	2.8	empty	no data	no data
1978	B	4	Undamaged	1.5	empty	no data	no data
1978	B	17	Undamaged	2.2	empty	no data	no data
1978	B	18	Undamaged (decayed)	2.2	empty	no data	no data
1978	B	16	Undamaged	2.7	empty	no data	no data
1978	A	31	Pecked head (and emaciated)	3.8	empty	no data	present
1979	B	8	Undamaged (fresh)	2.0	empty	none	none
1979	B	6	Undamaged (decayed)	1.7	empty	trace	none
1979	B	6	Undamaged (fresh)	1.6	empty	none	none
1979	B	2	Undamaged	1.6	few bones	none	none

Appendix Table II: (continued)

Year	Hatching Order	Age When Found	External Condition	Exposed Culmen Length	Stomach Contents		Parasites (Hirudinea)
1979	A	8	Undamaged	1.6	empty	1 cm. diameter	none
1979	C	4	Undamaged	1.7	empty	none	none
1979	B	12	Undamaged	2.5	empty	none	none
1979	B	5	Undamaged	1.6	empty	1 cm. diameter	none
1979	B	2	Undamaged	1.5	empty	2-3 cm. diameter	none
1979	B	12	Undamaged (fresh)	2.5	empty	none	15 in mouth and throat
1979	B	0	Squashed in nest, yolk sac ruptured	1.4	1 large fish bone	ruptured	none
1979	B	11	Undamaged (fresh)	2.2	empty	none	none
1979	B	4	Body flattened in nest	1.5	empty	none	none
1979	B	10	Undamaged	2.0	empty	none	none
1979	A	13	Undamaged (decaying)	2.4	empty	none	none
1979	C	6	Undamaged (decaying)	1.5	no data	no data	no data
1979	B	11	Undamaged (decaying)	2.0	empty	none	none
1979	B	4	body squashed (decaying)	1.6	some flesh and bones	none	none
1979	A	10	Undamaged (decaying)	2.2	few fish vertebrae	none	4 in mouth and throat
1979	B	7	Undamaged (decaying)	1.9	empty	none	none
1979	B	7	Undamaged (decaying)	1.7	empty	trace	none
1979	A	17	Undamaged	2.9	empty	none	none
1979	A	6	Flattened at nest edge	no data	some bones and flesh	no data	no data
1979	B	5	Wet and squashed	no data	empty	no data	no data
1979	B	0	Flattened in nest	1.5	empty	1 cm. in diameter	none
1979	B	19	Undamaged	2.6	empty	none	none

Appendix Table II: (continued)

Year	Hatching Order	Age When Found	External Condition	Exposed Culmen Length	Stomach Contents		Parasites (Hirudinea)
1979	A	10	Dead and stuck in *Urtica*	2.4	full of fish flesh	none	7 in mouth and throat
1979	B	25	Undamaged	2.7	empty	none	none
1979	A	30	Undamaged	3.7	empty	none	present
1979	B	22	Undamaged (fresh)	2.8	empty	none	no data
1979	A	35	Undamaged	no data	no data	no data	no data
1979	A	26	Undamaged	no data	no data	no data	35 in mouth
1979	A	19	Undamaged (decaying)	3.6	few fish bones	none	present
1979	A	21	Body flattened	2.9	few fish bones	none	none
1979	B	38	Undamaged	3.6	empty	none	no data
1979	A	34	Undamaged	3.8	few fish bones	none	11 in mouth
1979	A	50	Anterior part of tibia broken	4.5	few fish bones	no data	no data
1979	B	57	Left heel swollen	3.9	empty (stomach small)	none	28 in mouth
1979	A	15	Undamaged	2.2	empty	none	present

Appendix Table III: Result of Film Analysis' of Agents Causing Disappearance of Chicks in 1979

Case Number	Hatching Order	Number of Siblings Surviving	Age Last Recorded during Nest Check	Possible Agent and Comments
1	A	1	8	Ring-billed Gull walked to the nest area; head down, near nest; parents upset (calling and shifting aggressively and excitedly); Gull flew off directly after its intrusion on the nest.
2	B	1	8	Possibly a nocturnal loss; both chicks seen one evening; the next morning only one chick was seen.
3	A	1	0	Possibly a nocturnal loss; parents were upset (see case #1) at dawn one morning; no other unusual events were observed.
4	B	0	4	Agent of loss not seen; normal brooding behavior was observed for about one hour following a nest check; then the parent became jumpy, less attentive; brooding behavior was sporadic thereafter.
5	B	0	Not yet hatched	Ring-billed Gull was observed with its head down in the nest while the parents were absent; the Ring-billed Gull left within 40 sec and returned (or another arrived) five min later and appeared to eat something at the nest; the parents abandoned the nest; egg shell remains suggested that the chick had hatched; the sibling had died while pipping.

Appendix Table III: (continued)

Case Number	Hatching Order	Number of Siblings Surviving	Age Last Recorded during Nest Check	Possible Agent and Comments
6	B	1	3	Possibly a nocturnal loss; the brood shifted position away from the nest; parents were away for extended periods; nothing unusual was observed.
7	B	1	0	Possibly a nocturnal loss; nothing unusual noted.
8	B	1	11	Possibly nocturnally scavenged; chick wandered into a neighboring tern territory; was attacked and apparently killed by the neighboring adult Caspian Tern; the body was missing during the nest check.
9	B	1	5	Herring Gull plunged into the nest from the air and flew off before the next camera frame; parents were upset (see case #1); both chicks were present just before the attack and one was missing 16 min later during the nest check.
10	A	0	1	Possibly a nocturnal loss; the sibling egg was addled and parents continued to incubate it even after the chick disappeared; nothing unusual was observed.
11	A	0	0	Possibly predation, agent not seen; parent was behaving normally; suddenly became upset (calling aggressively, attacked a neighboring adult tern; then it lost all attentiveness to the nest, only returning sporadically.

Appendix Table III: (continued)

Case Number	Hatching Order	Number of Siblings Surviving	Age Last Recorded during Nest Check	Possible Agent and Comments
12	A	1	4	Possibly a nocturnal loss; nothing unusual was observed.
13	B	0	8	Cause of loss unknown; nothing unusual was observed but chick mobility made it difficult to observe and much was missed.
14	B	1	1	Possibly Ring-billed Gull predation; Ring-billed Gull was observed flying from the nest; Caspian Terns in the area were in alert (necks stretched) postures; the parent and one neibor were calling in the direction of the gull; afterwards only one chick was observed.
15	A	1	1	Possibly a nocturnal loss; a Ring-billed Gull was within 0.5 m of the nest at one time but little reaction by the parent was observed; no visible signs of scavenging occurred; after this nothing unusual was observed.